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DEPARTMENT OF COMMERCE

BULLETIN
OF THE
UNITED STATES BUREAU OF FISHERIES

VOL. XXXVII
1919-1920

HUGH M. SMITH
COMMISSIONER

WASHINGTON
GOVERNMENT PRINTING OFFICE
1922

Museum

CONTENTS.

Page.

✓ EARLY HISTORY AND SEAWARD MIGRATION OF CHINOOK SALMON IN THE COLUMBIA AND SACRAMENTO RIVERS. By Willis H. Rich. (Document 887, issued July 26, 1920)......... 1–74

NATURAL HISTORY AND PROPAGATION OF FRESH-WATER MUSSELS. By R. E. Coker, A. F. Shira, H. W. Clark, and A. D. Howard. (Document 893, issued May 2, 1921)........... 75–182

PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF SALMONOID FISHES AND THEIR SIGNIFICANCE IN FISH-CULTURAL PRACTICES. By William Converse Kendall. (Document 901, issued March 28, 1921).. 183–208

FURTHER LIMNOLOGICAL OBSERVATIONS ON THE FINGER LAKES OF NEW YORK. By Edward A. Birge and Chancey Juday. (Document 905, issued October 8, 1921)................. 209–252

DISTRIBUTION AND FOOD OF THE FISHES OF GREEN LAKE, WIS., IN SUMMER. By A. S. Pearse. (Document 906, issued October 7, 1921)...................................... 253–272

GENERAL INDEX.. 273–277

GENERAL INDEX.

Page.
Ambloplites rupestris, distribution and food ... 256, 259, 262, 268, 269
Ameiurus natalis, distribution and food ... 256, 263, 268, 269
  nebulosus ... 256, 263, 268, 269
Amia calva, distribution ... 256
Andalusia Chute, Mississippi River, mussels .. 97, 104, 109, 119
Auglaize River, mussels ... 92, 93

Birge, Edward A., and Chancey Juday: Further limnological observations on the Finger Lakes of New York 209–252
bluegill, distribution and food ... 256, 259, 264, 268, 269
Boleosoma nigrum, distribution and food ... 256, 263, 268, 269
bream, distribution and food ... 269
bullhead, speckled, distribution and food ... 256, 263, 268, 269
  yellow ... 256, 263, 268, 269

Caddo Lake, La. and Tex., mussels ... 98, 109
Calumet Deep River, mussels ... 95
Canandaigua Lake, N. Y., limnological observations (*see* Finger Lakes, N. Y.) ... 209–252
capelin, oviduct ... 191
carp, German, distribution and food ... 256, 259, 263, 268, 269
Catostomus commersonii, distribution and food ... 256, 259, 263, 268, 269
Cayuga Lake, N. Y., limnological observations (*see* Finger Lakes, N. Y.) ... 209–252
Center Lake, Ind., mussels ... 102
Chicago River, mussels ... 96
Chillicothe, mussels ... 109
chinook salmon, early history and seaward migration in Columbia and Sacramento Rivers ... 1–74
  alevins, planting ... 69
  appearance ... 69
  bibliography ... 71
  California coastal streams, collections ... 42
  care of fry ... 68, 69
  coastal streams, California and Oregon, collections .. 42
  Columbia River collections ... 7
  fall runs ... 5
  females and males, relative sizes ... 66
  fry, care of ... 68, 69
    length ... 70
    liberation from hatcheries ... 69, 71
    planting ... 68
  growth, rapid periods of ... 51
    rate of ... 45, 70
  investigation, history of ... 3
    methods ... 6
    problems ... 5
  length, estimated at beginning of intermediate growth ... 14, 48
    fry ... 70
    yearlings ... 70
  liberation of fry from hatcheries ... 69, 71
  males, precociously mature ... 69, 71
  males and females, relative sizes ... 66
  migration ... 47, 48, 49, 53, 57, 60, 62, 70
  miscellaneous collections ... 42
  Oncorhynchus tschawytscha ... 3

chinook salmon, etc.—Continued. Page.
  Oregon coastal streams, collections ... 42
  planting ... 68, 69
  plates, explanation of ... 72
  practical suggestions ... 68
  problems, statement of ... 5
  rate of growth ... 45, 70
  Sacramento River collections ... 32
  scales—
    analysis ... 6
    annuli ... 6
    bands ... 6, 25, 26, 49, 53, 54, 57, 58, 60, 70
    check, migratory ... 18
    check, primary ... 18, 54, 59, 70
    circuli ... 6
    Columbia River data ... 52
    development of ... 51
    generalizations ... 53
    growth, intermediate ... 13, 14, 25, 29, 53, 57, 60
    growth, new ... 25, 26, 53, 59, 60
    hatchery specimens ... 9, 53
    intermediate band ... 26, 53, 54, 57, 58, 70
    intermediate growth ... 13, 14, 25, 29, 53, 57, 60
    intermediate rings ... 12
    length ... 70
    measurement unit ... 6
    migratory check ... 18
    new growth ... 25, 26, 53, 59, 60
    photographs ... 6
    primary check ... 18, 54, 59, 70
    rings ... 6, 12, 25, 53, 54, 58, 59, 60, 70
    Sacramento River data ... 59
    summer band ... 6, 54, 60
    winter band ... 6, 25, 49, 54, 60, 70
  sex, proportions ... 65
    variations ... 65
  spring runs ... 5
  summary ... 70
  yearlings, length ... 70
cisco, distribution and food ... 256, 259, 265, 268, 269
Clark, H. W., observations on food of mussels ... 91
Clark, H. W., et al.: Natural history and propagation of fresh-water mussels ... 75–182
Clinch River, Tenn., mussels ... 84, 109
Cobitis, genital organs ... 191
  barbatula ... 191
  tænia ... 189, 191
Coker, R. E., et al.: Natural history and propagation of fresh-water mussels ... 75–182
Columbia River, seaward migration of chinook salmon in. 1–74
Coregonidæ, peritoneal membranes, ovaries, and oviducts ... 197, 200
Coregonus, peritoneal membranes, ovaries, and oviducts ... 189, 197
crappie, distribution and food ... 259, 269
Cumberland River, mussels ... 97, 109
Cyprinus carpio, distribution and food ... 256, 259, 263, 268, 269

Page.
Des Moines River, mussels........ 114
Detroit River, mussels........ 99
Distribution and food of fishes of Green Lake, Wis., in summer........ 253–272
    bibliography........ 272
dogfish, distribution........ 256

Early history and seaward migration of chinook salmon in Columbia and Sacramento Rivers........ 1–74
eel, genital organs........ 189, 191
elasmobranchs, relationship to salmonoids........ 200
Esox lucius, distribution and food........ 256, 259, 263, 268, 269
Eupomotis gibbosus, distribution and food... 256, 264, 268, 269

Fairport (Iowa) Fisheries Biological Station, mussels... 80, 84, 92, 93, 94, 100, 109, 114, 121, 125, 126, 127, 137, 138, 140, 143, 150, 155, 159, 160, 163, 165
Feeder Canal, Fort Wayne, Ind., mussels........ 84, 92, 101
Finger Lakes, N. Y. (Canandaigua, Cayuga, Seneca), limnological observations........ 209–252
    absorption of sun's energy........ 223
    bottom fauna........ 250
    distribution of heat........ 218, 223, 233, 234, 235
    epilimnion........ 213
    Green Lake, Wis., bottom fauna comparison........ 251
        plankton comparison........ 236, 237, 238, 239, 240, 241, 245, 247, 248, 249
    heat budgets........ 211
    heat distribution........ 218, 223, 233
        direct work........ 219
        distributed work........ 221
        heat and work as measured at depth........ 222
        subtraction curves........ 221
        work of sun and wind........ 218, 234, 235
    hypolimnion........ 213
    Lake Mendota, Wis., plankton comparison........ 241, 242
    literature cited........ 252
    macroplankton........ 235
    methods of plankton collection........ 235
    microplankton........ 235
    nannoplankton........ 235, 241, 249
    net plankton........ 235, 236, 243
    phytoplankton........ 236
    plankton........ 235, 250
        collection, methods........ 235
        tables........ 243
    radiation, transmission and transparency of........ 232
    summer heat income........ 215, 222, 223
    sun, work in distribution of heat........ 218, 234, 235
    sun's energy, absorption of........ 223
        transmission of, by waters of the various lakes.. 224, 228, 230, 231
    thermal regions........ 213
    thermocline........ 213
    transmission, of radiation........ 232
        of sun's energy by waters of the various lakes... 224, 228, 230, 231
    transparency of radiation........ 232
    wind, work in distribution of heat........ 218, 234, 235
    zooplankton........ 236
fish culture, salmonoids........ 203
fishes, general:
    conservation........ 155
    genital organs........ 188
    hosts of mussels........ 120, 137, 148, 151, 155, 162
    rescued from overflowed lands........ 162
fishes of Green Lake, Wis., in summer, distribution and food........ 253–272
    bibliography........ 272
    comparison with fishes of Lake Mendota.. 261, 269, 270, 271
    distribution........ 256, 270
    food........ 262, 266, 269, 271
    gill-net catches, 1919........ 257, 258, 261, 270
    species caught........ 256
    stratification........ 270
fishes of Lake Mendota, Wis., in summer, distribution and food:
    comparison with fishes of Green Lake..... 261, 269, 270, 271
    food........ 269, 271
    gill-net catches, 1919........ 259, 260, 261, 269, 270
    species caught........ 259
food, and distribution, of fishes of Green Lake, Wis., in summer........ 253–272
Fundulus diaphanus menona, distribution and food.... 256, 264, 268, 269
Further limnological observations on the Finger Lakes of New York........ 209–252
    literature cited........ 252

Galaxidæ, genital organs........ 190
ganoids, relationship to salmonoids........ 200
gar, distribution and food........ 259, 269
Grand River, Mich., mussels........ 84, 95, 102, 104, 109, 110, 118
Great Lakes, mussels........ 99
Great Lakes drainage, mussels........ 80, 82, 167
Green Lake, Wis.:
    bottom fauna........ 251, 271
    description........ 255, 270
    fishes (*see* fishes of Green Lake, Wis., in summer).. 253–272
    hydrographic map........ 254
    plankton........ 235
    shallow waters compared with those of Lake Mendota........ 271
    temperatures, summer 1919........ 255
Gulf of Mexico drainage, mussels........ 82

Holston River, Tenn., mussels........ 109
Homer, Minn., mussels........ 89, 102, 125
Howard, A. D., et al.: Natural history and propagation of fresh-water mussels........ 75–182

Illinois River, mussels........ 109, 124
Indiana lakes, mussels........ 99, 102
industrial wastes, harmful effects........ 124

James River, N. Dak. and S. Dak., mussels........ 96
Johnny darter, distribution and food........ 256, 263, 268, 269
Juday, Chancey, and Edward A. Birge: Further limnological observations on the Finger Lakes of New York 209–252

Kankakee River, mussels........ 104
Kendall, William Converse: Peritoneal membranes, ovaries, and oviducts of salmonoid fishes and their significance in fish-cultural practices........ 183–208

Lake Amelia, Minn., mussels........ 92
Lake Erie, mussels........ 99, 100
Lake Maxinkuckee, Ind., mussels........ 83, 85, 92, 98, 109, 122
Lake Mendota, Wis.:
    bottom fauna........ 271
    description........ 258, 270
    fishes (*see* fishes of Lake Mendota, Wis., in summer).. 259, 260, 261, 269, 270, 271
    mussels........ 98, 103, 108

Lake Mendota, Wis.—Continued. Page.
- nannoplankton, 241, 242
- shallow waters compared with those of Lake Green, 271
- temperatures, summer 1919, 259

Lake Michigan, mussels, 108
Lake Michigan, Traverse Bay region, mussels, 99
Lake Pepin, Minn., mussels, 88, 89, 93, 97, 98, 103, 108, 109, 118, 141, 159, 164
Lake Pokegama, Minn., mussels, 91, 118
Lake St. Clair, Mich., mussels, 99
Lakes of Middle Western States, mussels, 98
Lakes of Upper Central States, mussels, 99
lamprey, genital and visceral organs, 188, 189
largemouth black bass, distribution and food, 256, 259, 265, 268, 269
Lepidosteus, genital and visceral organs, 188, 201
Lepisosteus osseus, distribution and food, 259, 269
Lepomis incisor, distribution and food, 256, 259, 264, 268, 269
Leucichthys:
- birgei, distribution and food, 256, 265, 268
- peritoneal membranes, ovaries, and oviducts, 197
- sp., distribution and food, 259, 269

limnological observations on the Finger Lakes of New York (*see* Finger Lakes, N. Y.), 209–252
loach, ovary, 191
Lost Lake, Ind., mussels, 92
Lyons, Mich., mussels, 110

Madison, Ark., mussels, 109, 128
Mallotus, oviduct, 191
Maumee River, mussels, 92, 111
Micropterus dolomieu, distribution and food, 256, 265, 268, 269
- salmoides, 256, 259, 265, 268, 269

migration, seaward, of chinook salmon in Columbia and Sacramento Rivers, 1–74
Minnesota streams, mussels, 108, 110, 118
minnow, distribution and food, 269
- blunt-nosed, 256, 266, 268

Mississippi River, mussels, 80, 84, 89, 92, 93, 96, 97, 98, 100, 102, 104, 109, 110, 112, 114, 115, 118, 119, 120, 125, 127, 137, 163, 167
Missouri River, mussels, 96, 99, 102, 114, 123
Murænidæ, genital organs, 188, 190, 191
mussels, fresh-water, natural history and propagation, 75–182
- animal associates, 119
- breeding, 85
  - age begun, 137
  - brood pouches, 138
  - deposition of eggs, seasons, 140
  - fertilization, 138
  - incubation of eggs, seasons, 140
  - marsupia, 138
  - ovulation, 138
- byssus, species known to have, 158
- Chillicothe, 109
- commensalism, 119, 120
- commercial species, 98, 101, 107, 141, 152, 154
- competition for food, 120
- conditions of existence, 81
- conservation, 80, 155
- culture, 137, 163
  - aquaria, 94, 137, 163, 165
  - crates, 84, 109, 127, 137, 159, 164
  - pens, 164
  - ponds, 101, 125, 126, 127, 137, 159, 163, 164
  - tanks or troughs, 84, 92, 93, 125, 126, 165
- density of population, 84

mussels, fresh-water, etc.—Continued. Page.
- digestive gland, 173
- distribution (*see also* habitat)—
  - banks of streams, effects, 97
  - barriers in streams, effects, 96
  - horizontal, 97
  - longitudinal, 95
- diversity in form of shell, 170
- enemies, 122
- environment (*see* habitat), 94
- external features of shell, 168
- Fairport (Iowa) Fisheries Biological Station, ponds, tanks, etc., 80, 84, 92, 93, 94, 100, 109, 114, 121, 125, 126, 127, 137, 138, 140, 143, 150, 155, 159, 160, 163, 165
- Feeder Canal, Fort Wayne, Ind., 84, 92, 101
- feeding habits, 86, 114
- food, 79, 87
  - algæ, 88, 89, 90, 92, 93
  - animal matter, 90
  - Clark, H. Walton, observations, 91
  - competition for, 120
  - desmids, 92
  - detritus, 88, 90
  - diatoms, 88, 89, 92, 93
  - discrimination under normal conditions, 89
  - feeding habits, 86, 114
  - fish meat, 90
  - flagellates, 92
  - mineral matter, 88, 114
  - mud, 92
  - observations, 88, 90, 91, 93
  - organic matter, 88, 114
  - Palmellales, 90
  - pickerel blood, 90
  - plankton, 88, 92, 114
  - Schrader, Franz, observations, 88
  - Shira, A. F., observations, 93
  - significance of problem, 87
  - tadpole tails, 90
  - utilization of food materials, 89
  - vegetable matter, 89, 90
  - water content, 88, 114, 120
- form of shell, diversity in, 170
- foot, 173
- gills, 173
- glochidium, 143
  - ax-head type, 148
  - hooked type, 144
  - hookless or apron type, 144
  - mature, months found, 141, 142
- Gulf of Mexico drainage, 82
- habitat, 94
  - body of water, 94
  - bottom, 101
  - canals, 100
  - current, 111
  - depth, 107
  - dissolved gases, 117
  - lakes, 97, 101, 102, 103, 108, 111, 115, 117, 118, 124, 125
  - light, 110
  - marshes, 100
  - minerals in solution, 114
  - ponds, 100, 101, 103, 109, 115, 121, 124, 125, 126, 159, 165
  - sloughs, 100, 103
  - streams, 94, 101, 102, 105, 109, 111, 116, 117, 118, 123, 125

mussels, fresh-water, etc.—Continued.
  habitat—Continued. Page.
    swamps 100
    typical 119
    vegetation 118
    water content 113
  habits 79, 81
  heart 172
  Homer, Minn 89, 102, 125
  hosts 120, 137, 148, 151, 162
  infection 120, 137, 151
    optimum 162
  internal features of shell 169
  internal structure of soft body 173
  juvenile stage 84, 93, 118, 123, 137, 157
  labial palpi 173
  lakes—
    Caddo Lake, La. and Tex 98, 109
    Center Lake, Ind 102
    Great Lakes 99
    Great Lakes drainage 80, 82, 167
    Indiana lakes 99, 102
    Lake Amelia, Minn 92
    Lake Erie 99, 100
    Lake Maxinkuckee, Ind 83, 85, 92, 98, 109, 122
    Lake Mendota, Wis 98, 103, 108
    Lake Michigan 108
    Lake Michigan, Traverse Bay region 99
    Lake Pepin, Minn 88, 89, 93, 97, 98, 103, 108, 109, 118, 141, 159, 164
    Lake Pokegama, Minn 91, 118
    Lake St. Clair, Mich 99
    Lakes of Middle Western States 98
    Lakes of Upper Central States 99
    Lost Lake, Ind 92
    Oneida Lake, N. Y 103, 108, 110, 119
    Pike Lake, Ind 102
    Rice Lake, Wis 98
    Winona Lake, Ind 86, 102, 108, 109
  life history 79, 135–182
  lipfolds 173
  liver 173
  locomotion 79, 82, 118, 123
  Lyons, Mich 110
  Madison, Ark 109, 128
  mantle, form and functions 171, 173
  metamorphosis without parasitism 137, 156
  mouth 173
  natural history 81–134
  organ of Bojanus 173
  parasites 121
  parasitism 119, 120, 137, 148
    immunity 155
    metamorphosis without 156
  preying 119
  propagation 80, 135–182
  protection 80
  rectum 173
  rivers—
    Andalusia Chute, Mississippi River 97, 104, 109, 119
    Auglaize River 92, 93
    Calumet Deep River 95
    Chicago River 96
    Clinch River, Tenn 84, 109
    Cumberland River 97, 109
    Des Moines River 114
    Detroit River 99
    Grand River, Mich 84, 95, 102, 104, 109, 110, 118

mussels, fresh-water, etc.—Continued.
  rivers—Continued. Page.
    Holston River, Tenn 109
    Illinois River 109, 124
    James River, N. Dak. and S. Dak 96
    Kankakee River 104
    Maumee River 92, 111
    Minnesota streams 108, 110, 118
    Mississippi River 80, 84, 89, 92, 93, 96, 97, 98, 100, 102, 104, 109, 110, 112, 114, 115, 118, 119, 120, 125, 127, 137, 163, 167
    Missouri River 96, 99, 102, 114, 123
    Musselshell River, Mont 96
    Red River 82, 96, 99, 114, 123
    Rock Castle River 109
    Shell River, Minn 110
    St. Francis River, Ark 128
    St. Joseph River 92
    St. Mary River 92
    Yellow River, Ind 91
  shell 168
    abnormalities in growth 133
    calcareous layer 129
    diversity in form 170
    external features 168
    Fairport (Iowa) station 125, 126, 127
    formation 125, 129
    growth 125
    growth rings 129
    hypostracum 130
    internal features 169
    measurements of growth 125
    Mississippi River 125, 127
    mother-of-pearl layer 130
    nacreous layer 130
    periostracum 129
    prismatic layer 129
    rings 129, 132
    significance of rings 132
    St. Francis River, Ark 128
  soft body 171
  stomach 173
  structure 167
    internal 173
  symbiosis 119, 120
  unfavorable conditions for 133
    dams 97, 124
    dense vegetation 118
    drainage 123
    dredging 124
    droughts 123
    floods 123
    industrial wastes 124
    sedimentation 123
    sewage discharge 124
    shifting bottom 123
    stream barriers 96
    turbidity 114, 123
    wing dams 124
  winter habits 85
Musselshell River, Mont., mussels 96

Natural history and propagation of fresh-water mussels. 75–182
  bibliography 177
Neoceratodus, ventral mesentery 188
New York, limnological observations on Finger Lakes. 209–252
Notemigonus crysoleucas, distribution and food 269
Notopteridæ, genital organs 190
Notropis atherinoides, distribution and food 256, 266
  heterodon 269

Page.
Oncorhyncus, genital and visceral organs and membranes ... 188
  gorbuscha ... 188
  kisutch ... 188, 194
  nerka ... 188
  tschawytscha ... 188
Oncorhynchus tschawytscha, early history and seaward migration ... 3
  genital organs ... 188
Oneida Lake, N. Y., mussels ... 103, 108, 110, 119
Osmeridæ, genital and visceral organs and membranes .. 200
Osmerus, genital organs ... 191, 200, 201
  eperlanus ... 189
  mordax ... 197

Pearse, A. S.: Distribution and food of the fishes of Green Lake, Wis., in summer ... 253–272
Perca flavescens, distribution and food ... 256, 259, 266, 268, 269
Peritoneal membranes, ovaries, and oviducts of salmonoid fishes and their significance in fish-cultural practices ... 183–208
  works consulted ... 206
pickerel or Northern pike, distribution and food ... 256, 259, 263, 268, 269
pike, wall-eyed, distribution and food ... 259, 269
Pike Lake, Ind., mussels ... 102
Pimephales notatus, distribution and food ... 256, 266, 268, 269
Pomoxis sparoides, distribution and food ... 259, 269
Protopterus, ventral mesentery ... 188
pumpkinseed, distribution and food ... 256, 264, 268, 269

Rice Lake, Wis., mussels ... 98
Rich, Willis H.: Early history and seaward migration of chinook salmon in the Columbia and Sacramento Rivers ... 1–74
Red River, mussels ... 82, 96, 99, 114, 123
Roccus chrysops, distribution and food ... 259, 269
rock bass, distribution and food ... 256, 259, 262, 268, 269
Rock Castle River, mussels ... 109

Sacramento River, seaward migration of chinook salmon in ... 1–74
Salmo, genital and visceral organs and membranes ... 188
  fario ... 191
  gairdnerii ... 188
  salar ... 188, 196
  sebago ... 188
  shasta ... 188
  trutta ... 188
salmon, chinook (*see* chinook salmon) ... 1–74
Salmonidæ, genital and visceral organs and membranes. 187, 188, 189, 190, 191, 194, 200
salmonoid fishes, peritoneal membranes, ovaries, and oviducts and their significance in fish-cultural practices ... 183–208
  abdominal viscera ... 185
    supporting membranes ... 187
  air bladder ... 187
  alimentary tract ... 187
  anatomical facts, relation to fish culture ... 203
  Coregoni ... 189
  Coregonidæ ... 197, 200

salmonoid fishes, etc.—Continued. Page.
  Coregonus ... 197
  elasmobranchs, relationship ... 200
  fish-cultural practices, relation of anatomical facts to. 203
  ganoids, relationship ... 200
  genital organs, structure and development ... 188
  gonads ... 187, 189
  kidneys ... 187
  Leucichthys ... 197
  liver ... 187
  mesentery ... 187, 189
    dorsal ... 188
    ventral ... 188
  mesorchium ... 188
  mesovarium ... 188
  Oncorhynchus, species of ... 188, 194
  ovarian membranes ... 188, 189, 191
  ovaries ... 189, 190, 191, 197
  oviducts ... 189, 190, 194, 197, 200
  pancreas ... 187
  peritoneal membranes ... 197
  peritoneum and supporting membranes of viscera ... 187
  Salmo, species of ... 188, 191, 196
  Salmonidæ ... 187, 188, 189, 190, 191, 194, 200, 201
  Salvelinus, species of ... 188
  viscera, supporting membranes ... 187
  works consulted ... 206
Salvelinus, genital and visceral organs and membranes .. 188
  aureolus ... 188
  fontinalis ... 188
  kundsha ... 188
  malma ... 188
  marstoni ... 188
  oquassa ... 188
  stagnalis ... 188
Schrader, Franz, observations on food of mussels ... 88
Seneca Lake, N. Y., limnological observations (*see* Finger Lakes, N. Y.) ... 209–252
sewage discharge, harmful effects ... 124
Shell River, Minn., mussels ... 110
shiner, distribution and food ... 256, 266, 269
Shira, A. F., observations on food of mussels ... 93
Shira, A. F., et al.: Natural history and propagation of fresh-water mussels ... 75–182
smallmouth black bass, distribution and food .. 256, 265, 268, 269
smelts, genital and visceral organs and membranes ... 189, 190, 191, 194, 197, 198, 200, 201, 202
St. Francis River, Ark., mussels ... 128
St. Joseph River, mussels ... 92
St. Mary River, mussels ... 92
Stizostedion vitreum, distribution and food ... 259, 269
sturgeon, oviductless ... 189
sucker, common, distribution and food ... 256, 259, 263, 268, 269

top minnow, distribution and food ... 256, 264, 268, 269
trout, brown, genital organs ... 191
  fresh-water ... 189

white bass, distribution and food ... 259, 269
whitefishes, oviduct ... 189
Winona Lake, Ind., mussels ... 86, 102, 108, 109

yellow perch, distribution and food ... 256, 259, 266, 268, 269
Yellow River, Ind., mussels ... 91

59.7.13

EARLY HISTORY AND SEAWARD MIGRATION OF CHINOOK SALMON IN THE COLUMBIA AND SACRAMENTO RIVERS : : : : By Willis H. Rich

From BULLETIN OF THE BUREAU OF FISHERIES, Volume XXXVII, 1919–20

Document No. 887 : : : : : : : : : : : : : : : : : Issued July 26, 1920

PRICE, [illegible] CENTS

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UNITED STATES OF AMERICA

PRICE, 15 CENTS
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WASHINGTON : : : : : : GOVERNMENT PRINTING OFFICE : : : : : : : : : : 1920

CONTENTS.

Page.
- Introduction 3
  - History of the investigation 3
  - Statement of the problems 5
  - Methods 6
- Presentation of data 7
  - Fish from the Columbia River 7
  - Fish from the Sacramento River 32
  - Miscellaneous collections 42
- Conclusions 45
  - Rate of growth 45
  - Development of scales 51
  - Migration 62
  - Variations due to sex 65
    - Sex proportions 65
    - Relative sizes of males and females 66
    - Precociously mature males 67
- Practical suggestions 68
- Summary 69
- Bibliography 71
- Explanation of plates 72

EARLY HISTORY AND SEAWARD MIGRATION OF CHINOOK SALMON IN THE COLUMBIA AND SACRAMENTO RIVERS.

By WILLIS H. RICH,
Field Assistant, U. S. Bureau of Fisheries.

INTRODUCTION.

HISTORY OF THE INVESTIGATION.

The present study of the chinook salmon (*Oncorhynchus tschawytscha*), of which this paper forms the first contribution, was started in the summer of 1914 at the instance of the U. S. Bureau of Fisheries. The importance and necessity of such a study had been made apparent, especially by the work of Gilbert on the sockeye salmon, and it seemed advisable to extend in detail the outline of the life history of the chinook as given by Gilbert (1913). The method employed—that of analysis on the basis of scale studies—is now too well known and too widely used to need description. The paper just cited and subsequent studies of the sockeye by the same author contain a complete description of the methods employed and form admirable examples of studies prosecuted on this basis.

Our knowledge of the life histories of all the Pacific coast Salmonidæ was distinctly unsatisfactory previous to the discovery of the value of scale studies. The descriptions given by Jordan and Evermann (1896–1900), Jordan (1905), Rutter (1903), Scofield (1898), and Chamberlain (1907), contain the most accurate information regarding the chinook which was available prior to Gilbert's first study. The general features of the early life in fresh water and of the seaward migration were well known, and Chamberlain had shown quite conclusively that the sockeye and chinook salmon mature commonly at about the fourth year, although this is subject to variation. The work of McMurrich (1912) on the chinook salmon, based on the scales, has been shown by Gilbert (1913) to be unreliable because of the small number of specimens examined and an incorrect interpretation of the central (nuclear) area of the scales.

It remained, therefore, for Gilbert (1913) to give us the first accurate description of the general features of the life history of the chinook salmon in his paper, "The Age at Maturity of the Pacific Coast Salmon of the genus Oncorhynchus." In this he shows, among other things, that: (*a*) The chinook, or king, salmon spawn normally either in the fourth, fifth, sixth, or seventh year, the females more frequently in the fourth year; (*b*) the "grilse" are exclusively males and are of two sizes, representing two and three year fish; (*c*) the young may migrate as fry soon after hatching, or may remain in the stream until their second spring, migrating as yearlings; and (*d*) among the fish of any given age, the larger specimens will be those which migrated seaward as fry, although these do not attain the average stature of those fish, one year older, which migrated as yearlings.

In a recent paper Fraser (1917) has verified some of Gilbert's findings and has extended the study to the spring salmon found in the Straits of Georgia. He has worked out quite conclusively the rate of growth during the life in the sea and also the time of formation of the winter check.

The present study is a continuation of that begun by Gilbert, and the results thus far have been in perfect agreement with his, although the material has been much more abundant and diverse. The outline of the life history of the chinook as given by him may be almost indefinitely extended, but it seems most unlikely that results may be obtained which are not in agreement with his original conclusions.

At the beginning of this investigation it was supposed that an examination of the adult scales would give the data necessary for an understanding of the life history. Most of the summer and autumn of 1914 was, therefore, spent on the Columbia River collecting scales and data from adult fish. Small series of young, seaward migrants, were also taken at Astoria and Ilwaco, at the lower end of the Columbia estuary. Several collections of adult scales taken at spawning stations on various tributaries of the Columbia and Sacramento Rivers and collections of yearling chinooks made at Baird, Calif., were available for study through the courtesy of Dr. C. H. Gilbert. Access was also had to a collection of young migrants from the Sacramento River through the kindness of N. B. Scofield, of the California Fish and Game Commission. These various collections were studied during the winter and spring of 1914–15. It was possible to verify the main conclusions reached by Gilbert (1913), as follows: (1) The scales present two types of nuclear growth—one, the stream type, indicating that the fish migrated to the ocean after spending one year in fresh water, and the other, the sea type, indicating that the fish migrated as a fry; (2) the chinook may reach maturity at any time between the second and the seventh year. Those maturing in the second or third year are exclusively males.[a] The prevailing ages at which maturity is reached by the chinooks of the Columbia River are 4 and 5 years, although fish in their sixth year are fairly common. Specimens maturing in their seventh year are very rare.

Although it was possible to distinguish typical specimens of the two types of nuclear growth, it was found that there were many modifications of both types which were often confusing, although at the same time they were very significant. In the case of the young migrants taken in the Columbia estuary, the scales showed a well-defined area of narrower rings succeeded by a marginal band of wider rings. (See Pl. II, fig. 5.) At first it seemed that these fish must be in their second year; but this conclusion was not considered tenable, since, if this were true, the amount of growth which had taken place during the second year would be surprisingly small compared with that taking place in other cases where there was no doubt as to the proper interpretation of the scales. It seemed much more likely that the wide marginal rings represented a period of vigorous growth initiated by the young migrants on reaching the brackish water of the estuary. The problems presented were so complex that it was considered imperative that a careful study be made of the young migrants before proceeding further with the study of the mature fish.

To this end the writer undertook in the spring of 1915 the collection of the necessary data. As a result of unavoidable delay in getting a suitable net for this purpose, effective collecting was not begun until October. Collections were made chiefly on the lower Columbia between the mouth of the Willamette River and the ocean during October, November, and December, 1915. Owing to the unusually severe winter of 1915–16 the river contained so much ice that further collecting had to be deferred until March, 1916. From March until September frequent samples were taken at various points. These collections made in the Columbia River in 1914, 1915, and 1916, the collections from the Sacramento River mentioned above, and certain collections from the smaller coastal streams in California and Oregon contained in the Stanford University collection constitute the material on which this paper is based.

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[a] More recently females have been seen maturing in their third year, but in every case the scales indicated unmistakably that the fish had migrated as a fry. This is an important point for future consideration.

Thanks are due especially to Dr. C. H. Gilbert for assistance and advice given freely throughout the course of this investigation. The author is indebted also to Henry O'Malley, in charge of operations on the Pacific coast, and to Supts. Dennis Winn and Hugh C. Mitchell, of the U. S. Bureau of Fisheries, for advice and assistance in the collection of material. The friendly cooperation of the Oregon Fish and Game Commission, through Supt. R. E. Clanton, has also been of great assistance. John Larson, of the Oregon Fish and Game Commission, accompanied the writer on many of the collecting trips during 1916 and proved an invaluable assistant. To N. B. Scofield, of the California Fish and Game Commission, acknowledgment is due for permission to examine young salmon collected by him from the Sacramento River. Mrs. W. H. Rich aided in the preparation of scales for study and in the correction of manuscript.

STATEMENT OF THE PROBLEMS.

On beginning this work in June, 1914, the following tentative list of the more important problems relating especially to the Columbia River fisheries was made as a guide for determining the character of the future work:

1. What is the value of the hatchery work done on the river? Do the chinook fry planted from the hatcheries return as mature fish; and if so, when, and in what proportions?
2. At what ages do the young migrate to the ocean? What proportions migrate at the different ages, and what are the sizes of these migrants?
3. What age groups are represented in the different runs of the various species (chinook especially), and what are their average sizes and weights? Do these sizes and weights vary during the season?
4. What are the proportions in which these age groups are represented, and do the proportions vary during the season?
5. What are the relative sizes and proportions of males and females?
6. What results are being obtained from the marking experiments started in 1911 on the Sacramento River?

In addition to the above problems it was very soon found that one of the most important practical problems on the Columbia River has to do with the difference between the spring and the fall runs of chinook salmon. This has been kept in mind, therefore, throughout the work. The spring fish are much more valuable than the fall fish, being richer in oil and of better color, and the great desire of the commercial fisheries is to increase the spring run. It is obvious that the only opportunity to influence the history of the salmon is during the early life in fresh water before the young have migrated to the ocean. To do this intelligently, an exact knowledge of the early history, previous to migration, is necessary. The author has attempted, therefore, to give in this report as complete an account as possible of the early history of the chinook salmon. Important as these observations are, they are merely preliminary to the still more important study of the adult fish. Abundant material is at hand for this purpose, and the author hopes to present in the near future a report covering those problems which relate to the adult fish.

METHODS.

The methods usually employed at the present time in studies of the life histories of fish by means of scale analysis have been followed.

The length of the fish was determined by laying the specimen flat on a rule and measuring from the tip of the snout to the end of the middle rays of the caudal fin. These measurements were made in millimeters.

In counting the number of rings (circuli) on the scales the count has always been made in the anterior quadrant of the scale, since the number of rings has been found to be less variable there than in the lateral quadrants. The different areas of growth, such as the summer and winter bands (annuli), are also more sharply differentiated in the anterior quadrant.

Any measurements of scales and portions of scales which are given, were made by means of a camera lucida. The apparent image of the scale projected to the level of the base of the microscope was measured by a millimeter rule. There is obviously no significance to the actual size of this apparent image, since this would vary with the degree of magnification employed. The only value such measurements have is for comparative purposes. Therefore, the units of measurement have been considered as purely arbitrary, and no actual value is assigned. It seems hardly necessary to state that the same magnification has been used throughout this study. The actual magnification of the image was approximately × 120. This would give an actual value of 0.00834 mm. for each unit of measurement. The measurements as given in the tables were made from the center of the innermost ring along the anterior radius of the scale.

One method of study used has not, to the author's knowledge, been previously described. This is the employment of large series of photographs for the purpose of deciding doubtful points. It not infrequently happens that the scales from different lots of fish will vary consistently in one or more minor characters which are very difficult to determine by the successive examination of scales from individual fish. The memory seems incapable of carrying all the necessary details in such form that a logical conclusion could be reached. When, however, fairly large series of photographs, say 50 of each category, can be spread out side by side, the comparison may be made very readily, and often important conclusions may be drawn.

After some experimenting, in order to reduce the expense of plates, printing, etc., the scheme finally adopted for this purpose was to photograph directly on paper. Bromide paper was tried at first, but it did not prove satisfactory. Either Azo, F, hard X, or contrast Cyco was finally found to give the best results. Since the light values have no particular significance in scale photographs, where the main requirement is to show the lines well, these paper negatives are as favorable for study as prints taken from plates would be. In case duplicates are wanted, these negatives may be used in the same way as ordinary films and positive prints produced. The prints included with this report were made in this manner. A Leitz photomicrographic apparatus fitted with a 24-mm. mikro-summar was used and a small Bausch & Lomb arc lamp with condensing lens as a source of light. For the magnification used, 35 diameters, Azo, F, hard X requires an exposure of about 90 seconds and contrast Cyco about 15 seconds. The paper is placed in the regular plate holder behind a piece of clear glass. Another piece of glass or of stiff cardboard is placed behind the paper in order to hold it flat. The best focus is one which makes each line of the scale appear on the ground glass as a bright line having a narrow black line in the center. Considerable experience is necessary before one can obtain this focus properly. The size of the arc light will determine the amount of time required for a proper exposure, and the same size of arc should be used, therefore, for all photographs in a series. The printing requires an exposure to bright daylight (not sunlight) of about five seconds.

PRESENTATION OF DATA.

FISH FROM THE COLUMBIA RIVER.

The earliest collections made during any year were taken in the latter part of March and early in April, 1916. At this time a trip was made by launch from Portland to Astoria. Frequent hauls were made at different points, but many were unsuccessful because of the flood stage of the river. Also poor acquaintance with the river made it impossible to select the most favorable spots for seining. A seine 100 feet in length was used. This had half-inch mesh in the wings and one-fourth inch mesh in the bag The smallest salmon fry could be collected with this gear, as is proved by the fact that fry which had not completely absorbed the yolk sac were frequently captured. The later trips were more successful than the earlier ones, since the favorable places for seining had been learned and attention confined to these.

Collections were made March 31, 1916, at Mayger, Oreg., and at Grims Island, near Clatskanie, Oreg. On April 1 and 2 several collections were made at different points in the lower part of the Columbia estuary. The best collections were obtained on Sand Island and near Point Ellice, Wash. One hundred and forty-nine specimens in all were taken. Forty-seven of these were yearlings and 102 were fry. The study of the yearlings will have greater significance if delayed until after the development of the fry during the first year shall have been followed. The collections of fry made on this trip have all been studied separately, but no significant variations appeared, and the data are therefore presented in a single table (1).

Less than one-half of the fry had developed sufficiently to form even the central nuclear plates of the scales. Gilbert (1913*a*) describes a similar condition in the case of the migrating fry of the sockeye. Twenty-three individuals show the central platelets only and 19 have scales well enough developed for rings to be present. The average length[a] is 38.7 mm., with the mode at 38 mm. The average number of rings on the scales of the 19 specimens possessing scales sufficiently developed to show rings is 1.7. The average length of the anterior radius of the scales is 6.3 on the arbitrary scale. (See p. 6.) The following table (1) gives all the data regarding these collections.

---

[a] The averages employed in this paper are invariably the weighted mean.

TABLE 1.—FRY FROM LOWER COLUMBIA RIVER, MAR. 31 TO APR. 2, 1916.

Length.	Number.	Number of specimens with—		Scale record.[a]	
		Platelets only.	Scales with rings.	Average number of rings.[b]	Average length of anterior radius.[c]
46 to 50 mm.	2	0	2	3.0	20.5
41 to 45 mm.	19	4	6	2.0	8.5
36 to 40 mm.	71	17	9	1.3	5.1
31 to 35 mm.	10	2	2	1.5	4.2
Total	102	23	19		
Av. 38.7 mm.				1.7	6.3

[a] For units of measurement used in the scale records in this and all succeeding tables see explanation on p. 6.
[b] Estimated from those specimens only which have scales with rings.
[c] Estimated from all specimens with either scales or platelets.

It is apparent from this table that the scales are usually formed by the time the fish reach a length of 40 mm. It is not surprising that this condition is subject to a considerable amount of variation, especially when so few individuals are involved. The increase in the number of rings and in the size of the scales parallels the increase in total length of the fish.

Owing to the difficulty in sexing these small fry, no information is available regarding either sex proportions or variations due to sex.

A collection of 62 fry from the Clackamas hatchery, maintained near Oregon City, Oreg., by the U. S. Bureau of Fisheries, was made April 11, 1916. (See Table 2.) It will be interesting to compare this with the wild fish taken in the Columbia River. These hatchery fish average considerably larger than the wild individuals. This is presumably due, at least in part, to the warmer water in which they were hatched and reared. At the time this collection was made the water supply at the hatchery came from a spring, and the temperature was uniformly 50° F. throughout the year. None of the specimens are less than 40 mm. in length. The average is 46.5 mm., with the mode at 43 mm.

TABLE 2.—DATA FOR 62 FRY FROM CLACKAMAS HATCHERY, APR. 11, 1916.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
61 to 65 mm.	1	8.0	28.0
56 to 60 mm.	4	7.5	25.5
51 to 55 mm.	9	7.5	25.8
46 to 50 mm.	17	5.5	20.3
41 to 45 mm.	24	4.7	17.2
36 to 40 mm.	7	3.2	13.7
Av. 46.5 mm.		5.4	18.8

The obvious skewing of the curve of length toward the smaller sizes is probably due to constant additions to the smaller fish as a result of the hatching of the eggs spawned later in the season. The data at hand are not sufficient to prove this, however. Almost all the collections of small fry show such skewing which is apparently due to some such fundamental cause as the one suggested. The scales show a progressive increase in the number of rings and in the length of the anterior radius as the size of the fish increases. In comparison with the fry taken in March and April on the lower Columbia River, one is impressed by the fact that all of these hatchery fish, even the smallest, are provided with scales having well-developed rings. The smallest number of rings found on the scales of any specimen was three. A considerable proportion of the wild fish less than 45 mm. and more than 40 mm. in length have no scales, or at most only platelets. It seems likely that something in the conditions of life at the hatchery is responsible, but no direct evidence proved that this is available. The scales of the larger specimens have already acquired some of the characteristics of the scales of typical hatchery fish. Compared with the scales of wild fish, those from hatchery specimens show an irregular growth. There are frequent minor checks, indicated by narrower rings; but, as a rule, the true winter check is less well marked. The rings themselves are frequently slender and more or less broken. Plate I, figure 9, and Plate IV, figure 3, illustrate scales from hatchery fish. It is possible that a careful study of these characteristics might give a means of identifying adult fish which had been reared for the first few months under hatchery conditions.

In a collection of 26 fry from Cottonwood and Deer Islands, lower Columbia River, on April 13, 1916, the average length of the specimens is 43.2 mm., with the mode at 38 mm. (See Table 3.) The skewing of the curve toward the smaller sizes is even more marked in this collection than in the first one. The average length has increased 4.5 mm., but this seems largely due to the capture of several individuals which were considerably larger than any contained in the first collection, the one made on the lower river March 31 to April 2. The mode of the curve of length has remained the same. No important changes appear in the scale record, although, as would be expected from the larger average size of the fish, a slightly greater proportion has formed scales, and the average number of rings is greater.

Eighteen specimens were sexed. Males and females are in equal numbers, nine each. The average length of the males is 42.3 mm. and of the females 44.1 mm.

TABLE 3.—FRY FROM COTTONWOOD AND DEER ISLANDS, LOWER COLUMBIA RIVER, APR. 13, 1916.

Length.	Number.	Number of specimens with—		Scale record.	
		Platelets.	Scales with rings.	Average number of rings.	Average length of anterior radius.
66 to 70 mm.	1	0	1	6.0	23.0
61 to 65 mm.	1	0	1	8.0	23.0
56 to 60 mm.	1	0	1	5.0	18.0
51 to 55 mm.	2	0	2	4.0	25.5
46 to 50 mm.	0	0	0		
41 to 45 mm.	7	0	6	2.3	13.8
36 to 40 mm.	13	1	1	2.0	10.5
31 to 35 mm.	1	0	0		
Total	26	1	12		
Av. 43.2 mm.				3.3	17.1

A small series of 19 specimens was preserved at the Clackamas hatchery May 2, 1916. (See Table 4.) The average length is 46.7 mm., with the mode at 48 mm. All of the specimens have well-developed scales, none with less than four rings.

Ten of the specimens are males and have an average length of 46.5 mm. The nine females average 46.9 mm.

TABLE 4.—DATA FOR 19 FRY FROM CLACKAMAS HATCHERY, MAY 2, 1916.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
51 to 55 mm.	2	6	25.5
46 to 50 mm.	10	5.6	24.5
41 to 45 mm.	7	4.6	21.0
Av. 46.7 mm.	....	5.3	23.7

Several good collections were made May 10 and 11, 1916. These have been divided into two lots. The first was collected on Puget Island and at Crandall's seining ground on Grims Island. (See Table 5.) These points are located about 30 miles above Astoria. The second lot comprises collections made at several points on the lower part of the estuary, the best series coming from Sand Island and Point Ellice. (See Table 6.)

Two hundred and eighteen fry were taken at Crandall's seining ground and on Puget Island. Thirty-nine yearlings were taken at the same time. The length of the fry ranges from 33 to 98 mm. The average length is 52.5 mm., with the mode at 43 mm. The sex proportion in this collection is 54.1 per cent males to 45.9 per cent females. The average length of the males is 52.3 mm. and of the females 52.8 mm. The following table (5) contains the data for this collection:

TABLE 5.—FRY FROM CRANDALL'S SEINING GROUND AND PUGET ISLAND, LOWER COLUMBIA RIVER, MAY 10, 1916.

Length.	Number.	Number of specimens with—		Scale record.	
		Platelets.	Scales with rings.	Average number of rings.	Average length of anterior radius.
96 to 100 mm.	1	0	1	12.0	63.0
91 to 95 mm.	3	0	3	10.6	48.0
86 to 90 mm.	2	0	2	10.0	48.0
81 to 85 mm.	7	0	7	10.0	46.5
76 to 80 mm.	7	0	7	9.3	41.0
71 to 75 mm.	7	0	7	8.1	41.0
66 to 70 mm.	11	0	11	8.1	37.0
61 to 65 mm.	14	0	14	6.4	31.0
56 to 60 mm.	22	0	22	6.2	28.2
51 to 55 mm.	29	0	29	5.2	26.5
46 to 50 mm.	30	0	30	4.6	22.6
41 to 45 mm.	41	1	38	2.9	16.5
36 to 40 mm.	40	6	21	1.3	12.0
31 to 35 mm.	4	0	0	....	....
Total	218	7	192	....	....
Av. 52.5 mm.	....	....	....	4.9	22.4

The collections made May 11 in the lower part of the estuary include 103 fry and 10 yearlings. There are 52 males among the fry averaging 46.7 mm. in length. The 51 females average 48.8 mm. The following table (6) gives the data regarding the fry:

TABLE 6.—FRY FROM LOWER PART OF COLUMBIA ESTUARY, MAY 11, 1916.

Length.	Number.	Number of specimens with—		Scale record.	
		Platelets.	Scales with rings.	Average number of rings.	Average length of anterior radius.
81 to 85 mm.	1	0	1	9.0	43.0
76 to 80 mm.	0	0	0		
71 to 75 mm.	0	0	0		
66 to 70 mm.	0	0	0		
61 to 65 mm.	2	0	2	6.5	33.0
56 to 60 mm.	13	0	13	6.2	29.0
51 to 55 mm.	14	0	14	5.4	24.9
46 to 50 mm.	23	0	23	4.0	21.2
41 to 45 mm.	25	0	25	3.2	17.3
36 to 40 mm.	22	3	11	1.6	10.5
31 to 35 mm.	3	0	0		
Total	103	3	89		
Av. 47.7 mm.				4.2	20.6

In comparing these collections with the ones made the day before, the average smaller size of the fish is the only conspicuous point of difference. This is obviously due to a scarcity of fish of the larger sizes, since the modes of the two curves are the same, 43 mm. The water in the lower part of the estuary is quite brackish owing to the considerable admixture of salt water, while that in the part of the river where the collections of May 10 were made is perfectly fresh. Therefore it would seem probable that on reaching the brackish water the larger fish tended to continue their migration on into the ocean, while the smaller ones remained behind.

The next collection to be considered was made in the Columbia River near the mouth of the Little White Salmon River, about 50 miles above the point where the Willamette River joins the Columbia. This collection was made May 25, 1916, at which time 24 fry and 1 yearling were captured. The fry average 44.6 mm. in length and range from 37 to 61 mm. The mode is at 49 mm. Six specimens have no scales, 7 have only platelets, and 11 have scales with rings. Males and females are present in this collection in equal numbers and are also of equal size, both sexes averaging 44.6 mm. in length. The following table (7) contains the data:

TABLE 7.—FRY FROM COLUMBIA RIVER NEAR MOUTH OF LITTLE WHITE SALMON RIVER, MAY 25, 1916.

Length.	Number.	Number of specimens with—		Scale record.	
		Platelets.	Scales with rings.	Average number of rings.	Average length of anterior radius.
61 to 65 mm.	1	0	1	7.0	28.9
56 to 60 mm.	4	0	4	6.7	28.0
51 to 55 mm.	1	0	1	6.0	23.0
46 to 50 mm.	2	0	2	4.0	20.5
41 to 45 mm.	4	2	1	1.0	8.0
36 to 40 mm.	12	5	2	1.5	8.0
Total	24	7	11		
Av. 44.6 mm.				4.7	21.3

The smaller size of these fish as compared with those from below the mouth of the Willamette River is distinctly shown and is in accord with our explanation of the excessive proportion of small fish in the collections from the lower river; that is, that smaller fish are constantly being added to those in the estuary as a result of migration from above.

Eight specimens were preserved at the Clackamash atchery, May 27, 1916. These average 56 mm. in length. All have well developed scales. The average number of rings on the scales is 7.5, and the average length of the anterior radius of the scales is 28.5. There are four males averaging 53 mm. in length and four females averaging 59 mm.

A good collection of fry was made near Astoria, in the lower part of the estuary June 12 and 13, 1916. (See Tables 8 and 9.) In all, 132 specimens were taken, and it is worthy of note that none were yearlings. Yearlings do not appear in any subsequent collection from the lower part of the river, and it may be concluded from this that the yearling migrants quit the river for salt water about the first of June, if not earlier. This point is given more detailed consideration later.

Thirty-six of these fry were taken just within the mouth of a small creek near Point Ellice. They differ so distinctly from the remainder of the collection that they are considered separately. (See Table 8.) The average length is but 47.7 mm., with the mode at 38 mm. All of the individuals have formed scales, and in all but one, rings are present on the scales. The average number of rings is 4.1, and the average length of the anterior radius is 20.5. Nineteen of these specimens are males averaging 47.5 mm. in length. Seventeen females average 48 mm.

TABLE 8.—FRY FROM WITHIN MOUTH OF SMALL CREEK NEAR POINT ELLICE, COLUMBIA RIVER, JUNE 13, 1916.

Length.	Number.	Number of specimens with—		Scale record.	
		Platelets.	Scales with rings.	Average number of rings.	Average length of anterior radius.
66 to 70 mm	1	0	1	8.0	33.0
61 to 65 mm	2	0	2	7.0	28.0
56 to 60 mm	4	0	4	7.0	29.2
51 to 55 mm	7	0	7	5.3	25.0
46 to 50 mm	6	0	6	4.3	20.5
41 to 45 mm	5	0	5	3.4	18.0
36 to 40 mm	11	1	10	1.5	13.0
Total	36	1	35		
Av. 47.7 mm				4.1	20.5

The remaining 96 specimens collected in the estuary at this time are distinctly larger, averaging 76.5 mm. in length. In these specimens it is found for the first time that the scales of some of the fish have developed the wider marginal rings which have been designated "intermediate rings." This marginal band of wider rings is usually sharply differentiated from the central part of the scale and begins abruptly—not by a gradual increase in the space between rings. It may even be preceded by a slight narrowing, especially in the older fish. Gilbert (1913) has found similar intermediate growth in sockeye and silver salmon which migrated as yearlings. These intermediate rings represent a period of growth more rapid than the normal growth in fresh water and yet not so vigorous as the true ocean growth (Pl. II, figs. 3, 4, 5, and 6). Intermediate rings are not present on the scales of every specimen, but among the larger fry and yearlings taken in the estuary after the first of June some are always found which show this type of growth at the margins of the scales. For the purpose of ready comparison those fish whose scales show the band of intermediate rings are given separate consideration.

The fry contained in the collection of June 13 which do not show this intermediate growth (80 in number) average 75.2 mm. in length. The length ranges from 53 to 105 mm., with the mode at 73 mm. The average number of rings is 9.6, and the average length of the anterior radius is 38.1. The males number 35 (44 per cent) and average 78.3 mm. The 45 females average 72.8 mm. in length.

Sixteen specimens have scales which show the intermediate growth. These average 83.1 mm. in length. Seven males average 80.3 mm.; and 9 females, 85.3 mm. The following table (9) presents the data for this collection:

TABLE 9.—FRY FROM COLUMBIA ESTUARY, JUNE 12 AND 13, 1916.

EIGHTY SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
101 to 105 mm.	1	11.0	48.0
96 to 100 mm.	0	....	....
91 to 95 mm.	6	12.5	50.5
86 to 90 mm.	8	11.2	43.6
81 to 85 mm.	14	10.5	41.9
76 to 80 mm.	8	10.1	38.0
71 to 75 mm.	18	9.2	36.7
66 to 70 mm.	11	9.0	35.0
61 to 65 mm.	7	7.6	30.8
56 to 60 mm.	6	7.0	28.8
51 to 55 mm.	1	4.0	28.0
Av. 75.2 mm.	....	9.6	38.1

SIXTEEN SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number.	Scale record.					Average estimated length of fish at beginning of intermediate growth.[a]
		Number of rings—			Length of anterior radius—		
		To intermediate growth.	In intermediate growth.	Total.	To intermediate growth.	Total.	
91 to 95 mm.	3	12.3	4.6	16.9	33.0	51.3	63.0
86 to 90 mm.	3	13.0	6.0	19.0	26.3	46.3	49.6
81 to 85 mm.	5	10.6	4.6	14.6	26.0	42.0	52.0
76 to 80 mm.	2	10.0	4.0	14.0	25.5	38.0	53.0
71 to 75 mm.	2	8.5	4.0	12.5	23.0	33.0	50.5
66 to 70 mm.	1	9.0	4.0	13.0	23.0	33.0	48.5
Av. 83.1 mm.	....	11.6	4.6	16.2	26.7	42.4	53.3

[a] For explanation of estimated length of fish in this and succeeding tables see p. 14.

The smaller size of the fish taken within the mouth of the creek near Point Ellice is of interest and may be accounted for by one of two hypotheses: (1) These may be fry which are just migrating from the stream into the Columbia estuary. It is not known definitely whether chinook salmon spawn in this stream, but it is rather unlikely. Two attempts were made to determine this, but only silver salmon were obtained. The stream is quite small and is not a typical chinook stream, being for the most part shallow and with sandy bottom. Furthermore, since the stream is so near the ocean, it should be expected, owing to the warmer and more equable climate, that development would be more rapid than in the higher tributaries. If this were the case, it would be expected, unless growth were modified by some other factor, such as racial difference, that the fish coming from this stream would average larger than those from the higher tributaries. (2) The more probable hypothesis is that the smaller individuals among the migrating fry have run up into the mouth of the stream. This might be for the sake of the probable greater safety in such a location or because of the reduced salinity of the water. It has been shown by Rutter (1903) that the larger fry are more resistant to the effects of salt water, and also that alternations in the salinity of the water are a distinct aid in accustoming the young fish to sea water. The second hypothesis, therefore, seems a reasonable explanation for the presence of the smaller fish in the mouth of this stream. It is quite probable that if these fish remain for any length of time in the fresh water of such a stream it will have a tendency to slow up the growth rate and result finally in developing irregularities of scale growth.

Among those fish taken in the Columbia estuary proper it has been shown that those specimens whose scales show a band of intermediate rings average larger than those whose scales do not show this band. Since the wider rings indicate a more vigorous growth this result was quite to be expected and hardly calls for special comment. It is worthy of note, however, that the estimated length of the fish at the time of beginning this intermediate growth is distinctly less than the length of those fish which have not begun this intermediate growth. This estimated length was found by the method invented by Dahl and since used to advantage by Gilbert, and also by Fraser. This method involves the following proportion:

Total length of scale : total length of fish : : the length of the scale at some particular point : the length of the fish at the time this point was at the periphery of the scale.

By applying this proportion to each individual it is found that in the 16 individuals which have formed an intermediate band the average length at the time this intermediate growth was begun was 53.3 mm. The average length of those fish present in the estuary at this time, but which have not begun the intermediate growth, is 75.1 mm. This shows that the fish whose scales do not have an intermediate band have arrived in the estuary more recently than those whose scales do show this band of wider rings. The greater length of the fish which have been longer in the estuary is the result of the more rapid rate of growth maintained in the estuary as compared with the slower growth in fresh water upstream. The cause of the accelerated growth in salt water is at present unknown but is probably due to the increase in the food supply. One other possibility suggests itself in explanation of the fact that some individuals do not show the more rapid intermediate growth, namely, some individuals may not respond as readily (or perhaps not at all) to the stimuli encountered in the estuary which, in other individuals, initiate the accelerated growth.

One hundred and sixty-six specimens of migrating fry were captured at Point Ellice, July 19, 1916. (See Table 10.) The average length is 92.1 mm., ranging from 60 to 128 mm., with the mode at 93 mm. It will be noted that here and in the subsequent tables there is very little skewing of the curve of length toward the lower end. This indicates, undoubtedly, that no more of the smallest fry are being added from the upper waters. This is proved by the fact that no fry less than 60 mm. in length were taken. Such fry as are entering the estuary from above must be more nearly the same size as the fish already in the estuary.

The scales of these fish show an average of 12.9 rings. One hundred and sixteen have started a more rapid intermediate growth, which is indicated on the scales by a marginal band of wider rings. There is an average of 7.6 rings within the intermediate band, the band itself comprising 5.3 rings. Seventy-six of the specimens are males, averaging 90.1 mm. in length. Ninety females average 93.6 mm.

TABLE 10.—FRY FROM POINT ELLICE, COLUMBIA ESTUARY, JULY 19, 1916.

FIFTY SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
111 to 115 mm.	3	14.3	66.3
106 to 110 mm.	1	11.0	48.0
101 to 105 mm.	4	15.0	56.7
96 to 100 mm.	8	13.2	52.8
91 to 95 mm.	10	12.6	48.0
86 to 90 mm.	5	10.6	43.0
81 to 85 mm.	10	10.5	40.5
76 to 80 mm.	5	11.4	40.0
71 to 75 mm.	1	10.0	33.0
66 to 70 mm.	1	10.0	33.0
61 to 65 mm.	1	9.0	33.0
56 to 60 mm.	1	9.0	28.0
Av. 89.9 mm.	....	11.9	46.4

ONE HUNDRED AND SIXTEEN SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number.	Scale record.					Average estimated length of fish at beginning of intermediate growth.
		Number of rings—			Length of anterior radius—		
		To intermediate growth.	In intermediate growth.	Total.	To intermediate growth.	Total.	
126 to 130 mm.	1	7.0	13.0	20.0	28.0	78.0	43.0
121 to 125 mm.	0	....	....	....	....	....	....
116 to 120 mm.	8	9.6	7.1	16.7	37.0	63.0	76.5
111 to 115 mm.	4	9.2	7.3	16.5	30.5	60.8	60.5
106 to 110 mm.	8	7.7	7.0	14.7	30.8	57.0	54.5
101 to 105 mm.	9	8.4	6.9	15.3	31.3	56.5	58.0
96 to 100 mm.	12	8.0	5.4	13.4	30.2	51.0	60.5
91 to 95 mm.	22	7.2	5.6	12.8	28.5	48.3	54.5
86 to 90 mm.	23	7.3	4.9	12.2	27.1	44.9	55.5
81 to 85 mm.	14	7.2	4.2	11.4	27.2	41.3	52.6
76 to 80 mm.	7	6.9	4.7	11.6	24.4	39.5	47.3
71 to 75 mm.	5	6.2	4.0	11.2	21.0	36.4	43.0
66 to 70 mm.	1	5.0	5.0	10.0	23.0	28.0	38.0
61 to 65 mm.	2	6.5	5.0	11.5	23.0	35.5	50.5
Av. 93.1 mm.	....	7.6	5.5	13.1	28.3	49.8	55.3

With few minor exceptions, the results obtained from the study of this collection are similar in all respects to those obtained from a study of the June collections. The difference in length between the fish which have begun the rapid intermediate growth and those which have not is less but is plainly indicated, the fish having the intermediate band being larger. The average estimated length at the time of beginning the intermediate growth is approximately the same, 55.3 mm.

A collection containing 51 specimens was made at Point Ellice, August 12, 1916. Another series of 13 specimens was collected from the same place August 26, 1916. Since no particular difference in these two collections has appeared as a result of their study, they will be considered together. (See Table 11.) The average length is 93.9 mm., ranging from 49 to 122 mm. The mode is at 93 mm. It will be noticed that the average length of this collection is approximately the same as that of the July collection. It might be concluded from this that an average length of 92 or 93 mm is the maximum attained in the estuary, but this conclusion is not borne out by subsequent collections. Forty of these specimens are males, averaging 92 mm. in length. Twenty-four females average 97.2 mm.

The scales do not differ greatly from those of the July collection. The number of rings has increased slightly, although the size of the scale, as indicated by the length of the anterior radius, remains practically the same. The estimated length at the time of beginning the intermediate growth is nearly the same as in June and July. Six of the specimens collected August 26 begin to show at the periphery of the scales narrow rings, indicating the slower winter growth.

TABLE 11.—FRY FROM POINT ELLICE, WASH., AUG. 12 AND 26, 1916.

TWENTY-SEVEN SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
106 to 110 mm	2	18.0	55.5
101 to 105 mm	1	14.0	48.0
96 to 100 mm	4	16.0	54.2
91 to 95 mm	5	14.4	47.0
86 to 90 mm	9	13.7	45.7
81 to 85 mm	1	14.0	43.0
76 to 80 mm	0		
71 to 75 mm	1	10.0	43.0
66 to 70 mm	2	10.0	38.0
61 to 65 mm	1	9.0	33.0
56 to 60 mm	0		
51 to 55 mm	0		
46 to 50 mm	1	4.0	18.0
Av. 87.8 mm		13.5	45.7

TABLE 11.—FRY FROM POINT ELLICE, WASH., AUG. 12 AND 26, 1916—Contd.

THIRTY-SEVEN SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number.	Scale record.					Average estimated length of fish at beginning of intermediate growth.
		Number of rings—			Length of anterior radius—		
		To intermediate growth.	In intermediate growth.	Total.	To intermediate growth.	Total.	
121 to 125 mm	1	13.0	7.0	20.0	38.0	63.0	73.0
116 to 120 mm	2	13.5	8.0	21.5	45.5	68.0	80.5
111 to 115 mm	2	13.0	7.5	20.5	38.0	55.5	73.0
106 to 110 mm	3	9.0	9.0	18.0	29.6	58.0	65.5
101 to 105 mm	8	9.1	7.3	16.4	29.6	54.2	58.0
96 to 100 mm	4	9.2	8.2	17.4	30.5	56.7	54.2
91 to 95 mm	9	6.2	9.3	15.5	22.3	51.3	44.1
86 to 90 mm	4	7.5	8.0	15.5	24.4	43.0	51.5
81 to 85 mm	3	6.0	5.8	11.8	23.0	38.0	51.3
76 to 80 mm	1	6.0	6.0	12.0	23.0	43.0	48.0
Av. 98.5 mm		8.5	7.9	16.1	28.2	52.3	54.8

Three specimens of young chinook salmon were caught August 23, 1916, by hook and line from the wharf of P. J. McGowan & Sons at Ilwaco, Wash. These young fish were under the cannery and were feeding voraciously on the offal resulting from the cleaning of the adult salmon. Their stomachs were quite filled with eggs and small pieces of kidney, flesh, etc. There was very little evidence that they had been feeding on insects or crustaceans. Several other collections were made under this cannery and one other in Astoria, and in every case the young fish were found to have eaten heavily of the offal. These three specimens are all females averaging 118 mm. in length. The scales of one specimen show a distinct intermediate band of eight rings. The average number of rings on the scales is 21.3. The length of the anterior radius averages 61.3.

Ten specimens of young chinooks were collected in the Clackamas River, August 30 and 31, 1916. (See Table 12.) The collection was made by hook and line near the Clackamas hatchery, about 2 miles above where the Clackamas River flows into the Willamette. Five of these are males averaging 113.8 mm. in length. The five females average 112 mm. Four of the males were approaching maturity, as was indicated by the enlarged and white testes. The average length of these four is 118.2 mm. The scales of these precocious males are in every respect similar to the scales of the other individuals. Such precociously matured males have been previously described by Rutter (1903). The scales of these fish indicate unmistakably that they were fry, less than 1 year old. The scales of 8 out of the 10 individuals show a distinct narrowing of the marginal rings corresponding to the slower growth of the fall and winter. Since the number of specimens is so small, no attempt is made to segregate the specimens showing different types of scale growth.

TABLE 12.—YOUNG CHINOOKS FROM CLACKAMAS RIVER, AUG. 30 AND 31, 1916.

Average length.	Number—		Scale record.				Average estimated length of fish at time of formation of check.
	Total.	With check.	Number of rings—		Average length of anterior radius—		
			To check.	Total.	To check.	Total.	
112.9 mm	10	7	6.7	20.7	17.3	58.2	43.4

The check found on these scales, while in some respects similar, can not be considered as identical with the check preceding the intermediate rings, which is a feature of the scale growth of the fish taken on the lower river. The central part of the scales, within the check, is composed of a fewer number of rings, is smaller in size, and the rings succeeding the check are not so wide. (See Pl. I, figs. 7 and 8.) While it seems probable that the fundamental causes underlying the formation of these checks are similar (probably a change in the food supply or other environmental conditions), the change in the case of the fish entering the brackish water of the estuary is more profound. In order to distinguish these two types of checks in the discussions, the term "primary check" will be used for that formed in the upper parts of the stream and "migratory check" for that formed on entering the estuary. The next collection to be mentioned will throw further light on this question.

In April and May, 1915, the Oregon Fish and Game Commission planted, from the hatchery at Bonneville, several carloads of chinook fry in a small artificial lake near Seufert, Oreg. The fish were fed daily with offal from Seufert Bros. cannery, which is located at this point. At the time the plant was made the writer measured a small series of the fish. The average length was 44.6 mm. September 2, 1915, a collection of 55 specimens was made by hook and line from this lake and the outlet which connected the lake with the Columbia River. (See Table 13.) The average length was 80.9 mm. Twenty-seven were males averaging 81.5 mm. in length and 28 were females averaging 80.3 mm. There were three mature males in the lot, and these averaged 94 mm. in length. The most interesting point which appeared in the study of this collection has to do with the formation of the primary check mentioned above. Such a check was apparent on the scales of 84 per cent of the specimens, and an average of 6.7 rings was included within this check. The general appearance of the scales is similar to that of fish reared under typical hatchery conditions; that is, the rings are more or less irregularly spaced and may be broken. (See Pl. I, fig. 6.) The central portion was missing from many of the scales examined, so that it was frequently necessary to examine several scales from the same fish before a perfect one was found. Not infrequently a similar central portion would be dislocated in reference to the scale as a whole, as though it had been loosened and turned within the delicate pocket of the skin in which the scale is formed. This appearance has also been described by Gilbert (1914, p. 62), who has found it on the scales of the sockeye salmon. These blank and dislocated centers correspond in size to the area within the check on the perfect scales, and there could be no doubt that the same cause was responsible for all three of these abnormalities in the scale growth. Nineteen specimens (35 per cent) had begun the slower winter growth, as is indicated by the narrower marginal rings. The following table (13) gives the data regarding this collection. No attempt is made to segregate the few specimens whose scales do not possess this primary check.

TABLE 13.—YOUNG CHINOOKS FROM LAKE AT SEUFERT, OREG., SEPT. 2, 1915.

Length.	Number—		Scale record.				Average estimated length of fish at time of formation of check.
	Total.	With check.	Number of rings—		Length of anterior radius—		
			To check.	Total.	To check.	Total.	
106 to 110 mm.	2	2	8.5	14.0	25.5	45.5	63.0
101 to 105 mm.	2	2	9.5	17.0	33.0	55.5	63.0
96 to 100 mm.	0	0					
91 to 95 mm.	3	3	5.6	13.6	21.3	41.3	49.5
86 to 90 mm.	7	7	8.3	14.6	28.8	44.4	54.5
81 to 85 mm.	12	11	6.7	12.9	22.5	39.2	46.0
76 to 80 mm.	11	8	6.1	12.3	21.1	37.5	45.0
71 to 75 mm.	12	7	5.6	11.4	17.3	32.5	41.0
66 to 70 mm.	5	5	6.4	11.2	18.0	31.0	39.0
61 to 65	1	1	4.0	11.0	13.0	28.0	33.0
Total	55	46					
Av., 80.9 mm.			6.7	12.7	22.2	37.9	47.9

The almost exact correspondence between the estimated length at the time of the formation of the primary check and the actual observed length at the time of planting proves conclusively that in this particular instance the altered rate of growth following the formation of the check was in response to the changed environmental conditions resulting from the removal of the fish from the hatchery at Bonneville to the lake at Seufert.

Sixty-nine specimens were collected September 15, 1916, at Crandall's seining ground on Grims Island. In several respects this is an unusual collection. The average length is but 74.4 mm., the smallest recorded since June. The proportion of specimens whose scales show the intermediate growth is also very small, only three in the entire collection. None of the other collections made at this point are remarkable for the small size of the fish as compared with other collections made at the same time of year in other localities, so that it is unlikely that selection has taken place here as was evidently the case with the collection made within the mouth of the small stream near Point Ellice. A possible explanation may be that we are dealing here with a series composed largely, if not wholly, of fish migrating seaward from some particular tributary or region of the Columbia River watershed, in which the fry do not attain, before migration, as large a size as is common for other parts of the watershed. Gilbert (1912*a*) has described such differences among the young migrating sockeyes in different tributaries of the Fraser River system. This explanation seems, therefore, plausible in the case of these young chinooks, although admittedly unproved.

The three specimens which show a band of intermediate rings are among the largest taken and average 89.3 mm. in length. The average number of rings preceding the intermediate growth is 7. The number of intermediate rings averages 9, and the average total number of rings is, therefore, 16. The average length of the anterior radius of the scale is 21.3 to the beginning of the intermediate growth and 47.3 to the periphery of the scales. The average estimated length at the time of beginning the rapid growth is 39.3 mm. The whole collection contains 36 males and 33 females. The males have an average length of 74.2 mm. and the females 74.8 mm. In the following table (14) are presented the data relative to those specimens whose scales do not show a band of intermediate rings:

TABLE 14.—DATA FOR 66 YOUNG CHINOOKS FROM CRANDALL'S SEINING GROUND, SEPT. 15, 1916.

SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Length.	Number.	Scale record.	
		Number of rings.	Length of anterior radius.
86 to 90 mm.	4	15.5	54.0
81 to 85 mm.	6	14.9	45.1
76 to 80 mm.	20	13.4	42.0
71 to 75 mm.	14	12.9	41.0
66 to 70 mm.	14	11.9	36.5
61 to 65 mm.	7	11.9	33.5
56 to 60 mm.	1	13.0	33.0
Av. 73.8 mm.	....	13.1	40.1

Thirty-five young chinooks were taken by hook and line September 17, 1914, from beneath the McGowan cannery at Ilwaco, Wash. The scales of 28 (80 per cent) of these show a marginal band of intermediate rings. As a rule these intermediate rings are distinctly heavier and wider than is the case with the average fish collected elsewhere in the estuary. It is also found that the rings immediately preceding the intermediate band are sometimes distinctly narrower than the more central rings. (See Pl. II, figs. 5 and 7.) This same appearance characterizes the scales of a few specimens from Crandall's seining ground, just mentioned, and, to anticipate, is found in varying proportions in all later collections from the estuary. There are not, however, two distinct categories of scales, one exhibiting a distinct narrowing preceding the intermediate growth and the other without such narrowing. All stages in the development of this band of narrow rings may be observed from examples where the intermediate band begins merely as a sudden widening (Pl. II, fig. 6) to those where the intermediate band is preceded by a very clear and well-marked band of narrow rings (Pl. II, fig. 5). Plate II, figure 7, represents an intermediate condition. Among the seven fish whose scales do not show intermediate growth are five whose scales terminate in narrow rings of the winter type. These are somewhat smaller than the specimens whose scales do show the intermediate band, and there can be little doubt that they are the more recent arrivals from upstream which had not yet begun the intermediate growth.

The scales of some of the specimens contained in this collection have also a more or less well-developed primary check in addition to the migratory check which immediately precedes the intermediate growth. This also is found in varying proportions in the subsequent collections and will be considered more in detail later. Eighteen males average 121.3 mm. in length and 17 females average 124.7 mm. The following table (15) contains the data for this collection:

TABLE 15.—YOUNG CHINOOKS FROM UNDER THE CANNERY, ILWACO, WASH., SEPT. 17, 1914.

SEVEN SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Average length.	Scale record.	
	Number of rings.	Length of anterior radius.
120.2 mm	20.2	59.4

TWENTY-EIGHT SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at beginning of intermediate growth.
		Number of rings—		Length of anterior radius—		
		To intermediate growth.	Total.	To intermediate growth.	Total.	
151 to 155 mm	1	17.0	28.0	53.0	88.0	98.0
146 to 150 mm	0					
141 to 145 mm	2	17.0	24.5	55.0	75.0	105.0
136 to 140 mm	1	25.0	30.0	53.0	78.0	98.0
131 to 135 mm	1	20.0	23.0	53.0	58.0	118.0
126 to 130 mm	6	17.0	20.7	48.0	61.0	100.0
121 to 125 mm	5	18.6	21.4	50.0	60.0	105.0
116 to 120 mm	6	16.6	20.3	47.0	59.0	95.0
111 to 115 mm	4	16.2	19.6	45.0	55.0	89.0
106 to 110 mm	0					
101 to 105 mm	2	13.0	19.5	40.0	60.0	70.0
Av. 123.5 mm		17.2	21.4	48.1	62.0	96.8

Seven specimens were collected from the Clackamas River near the hatchery on October 13, 1915. These were obtained by hook and line fishing, and the collection is too small and too variable to deserve detailed attention. The average length is 118 mm., and the average total number of rings on the scales, 21. Several show the primary check, and one at least had apparently started a new period of vigorous growth. This is indicated on the scales by a marginal band of five slightly wider rings. The scales of all of the other specimens terminate in rings of the winter type.

October 16, 1915, a collection consisting of 119 young chinooks was made at Point Ellice, Wash. The total average length is 112.7 mm. Sixty-one males average 112.2 mm. and 58 females 113.3 mm. Twenty-nine specimens (24 per cent) have a distinct intermediate band at the margins of the scales. The scales of the remaining 90 specimens terminate uniformly in narrow winter rings. The scales of a considerable proportion show the primary check about 9 or 10 rings from the center. The following table (16) presents the data.

TABLE 16.—YOUNG CHINOOKS FROM POINT ELLICE, WASH., OCT. 16, 1915.

SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Length.	Number—		Scale record.				Average estimated length of fish at time of formation of check.
	Total.	With primary check.	Number of rings—		Length of anterior radius—		
			To check.	Total.	To check.	Total.	
146 to 150 mm	1	1	16.0	30.0	53.0	93.0	88.0
141 to 145 mm	0	0					
136 to 140 mm	0	0					
131 to 135 mm	1	1	12.0	28.0	38.0	78.0	63.0
126 to 130 mm	2	2	9.0	29.5	28.0	70.5	50.5
121 to 125 mm	8	4	9.7	24.0	26.7	63.0	55.2
116 to 120 mm	19	12	10.6	23.8	30.0	61.7	61.7
111 to 115 mm	23	14	11.0	23.4	32.2	58.5	59.0
106 to 110 mm	23	17	10.0	22.0	28.5	58.0	54.0
101 to 105 mm	9	6	10.8	21.7	29.6	55.7	47.1
96 to 100 mm	4	3	10.3	21.5	26.3	53.0	51.3
Total	90	60					
Av. 113.0 mm			10.6	23.1	30.2	59.8	57.1

SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
	Total.	With primary check.	Number of rings—			Length of anterior radius—				
			To primary check.	To intermediate growth.	Total.	To primary check.	To intermediate growth.	Total.	Primary check.	Intermediate growth.
131 to 135 mm	2	1	9.0	22.0	25.5	28.0	58.0	68.0	53.0	113.0
126 to 130 mm	1	0		23.0	26.0		53.0	63.0		118.0
121 to 125 mm	1	0		19.0	24.0		48.0	63.0		93.0
116 to 120 mm	5	5	9.8	22.8	25.6	26.0	55.0	66.0	47.0	98.0
111 to 115 mm	5	5	10.6	21.8	25.2	29.0	50.0	60.0	55.0	96.0
106 to 110 mm	9	5	7.0	19.4	22.3	24.0	49.6	58.5	43.0	91.8
101 to 105 mm	4	1	11.0	18.2	21.7	33.0	46.7	56.7	53.0	85.5
96 to 100 mm	2	0		17.0	19.5		48.0	55.5		85.5
Total	29	17								
Av. 111.0 mm			9.25	20.3	23.4	26.8	50.7	60.6	48.9	94.7

In connection with the series just considered another collection made the following day, October 17, 1915, is of considerable interest. This second collection was made by hook and line under one of the canneries located at Astoria, Oreg., the Union Fishermen's Cooperative Cannery. As has been already mentioned, fish taken under these conditions are always found to be feeding heavily on the offal from the cannery. This collection consists of 61 specimens, of which 43 (70 per cent) have scales which show the intermediate growth. The average length of this collection is considerably greater than for the Point Ellice collection, 127.5 mm. The specimens which had begun the rapid intermediate growth average 130.5 mm., and those which had not done so average but 120.2 mm. All of the specimens whose scales do not show intermediate rings have the narrow winter rings at the scale margins. Thirty-three males average 127.9 mm. in length and 28 females 127.0 mm. The following table (17) gives the data for this collection:

TABLE 17.—YOUNG CHINOOKS FROM UNDER CANNERY, ASTORIA, OREG., OCT. 17, 1915.

SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Length.	Number—		Scale record.				Average estimated length of fish at time of formation of check.
			Number of rings—		Length of anterior radius—		
	Total.	With check.	To primary check.	Total.	To primary check.	Total.	
151 to 155 mm.	1	0	....	25.0	....	88.0	....
146 to 150 mm.	0	0	....	....	....	....	....
141 to 145 mm.	0	0	....	....	....	....	....
136 to 140 mm.	0	0	....	....	....	....	....
131 to 135 mm.	0	0	....	....	....	....	....
126 to 130 mm.	2	2	9.0	25.5	25.5	68.0	48.0
121 to 125 mm.	6	2	6.0	23.3	20.5	68.0	40.5
116 to 120 mm.	3	2	6.5	22.6	23.0	58.0	45.5
111 to 115 mm.	3	2	10.5	22.0	33.0	56.3	65.5
106 to 110 mm.	3	3	7.3	22.3	24.6	61.3	41.3
Total	18	11	....	....	....	....	....
Av. 120.2 mm.	....	....	7.8	23.2	25.2	64.5	48.0

SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
			Average number of rings—			Average length of anterior radius—				
	Total.	With check.	To check.	Intermediate growth.	Total.	To check.	Intermediate growth.	Total.	Check.	Intermediate growth.
176 to 180 mm.	1	0	....	22.0	34.0	....	73.0	113.0	....	118.0
171 to 175 mm.	0	0	....	....	....	....	....	....	....	....
166 to 170 mm.	0	0	....	....	....	....	....	....	....	....
161 to 165 mm.	0	0	....	....	....	....	....	....	....	....
156 to 160 mm.	1	1	9.0	23.0	28.0	28.0	58.0	73.0	63.0	123.0
151 to 155 mm.	2	2	9.5	24.0	28.5	30.5	65.5	88.0	53.0	115.5
146 to 150 mm.	3	3	10.3	24.3	29.3	33.6	66.3	83.0	58.0	118.0
141 to 145 mm.	3	2	12.0	24.0	29.0	35.5	64.6	81.3	63.0	109.6
136 to 140 mm.	3	2	8.5	22.3	26.9	28.0	58.0	79.6	50.5	106.3
131 to 135 mm.	8	6	7.1	22.9	27.0	23.0	58.0	73.0	43.0	106.1
126 to 130 mm.	5	4	10.2	21.6	26.0	30.5	59.0	73.0	53.0	106.0
121 to 125 mm.	9	6	8.1	20.4	23.8	26.5	56.3	69.2	45.8	103.0
116 to 120 mm.	3	3	10.3	20.4	23.0	31.3	51.3	59.6	63.0	104.6
111 to 115 mm.	2	2	8.9	20.0	24.0	23.0	50.5	60.5	45.5	90.5
106 to 110 mm.	1	1	9.0	19.9	24.9	28.0	43.0	63.0	48.0	78.0
101 to 105 mm.	1	1	13.0	22.0	24.0	33.0	53.0	58.0	63.0	93.0
96 to 100 mm.	1	0	....	14.0	15.0	....	48.0	53.0	....	93.0
Total	43	33	....	....	....	....	....	....	....	....
Av. 130.5 mm.	....	....	9.3	21.8	26.0	28.2	58.0	73.0	50.9	105.5

Four young chinooks were collected October 22, 1915, from the Little White Salmon River, Wash. These were taken near the hatchery maintained by the Bureau of Fisheries, which is about a half mile above the point where the Little White Salmon enters the Columbia River. These four fish are all females and average 92.5 mm. in length. The average number of rings on the scales is 15.8, and the average length of the anterior radius of the scales, 52.5. There is no indication of wider marginal rings on the scales of these fish.

A collection consisting of 100 specimens was made October 24 to 27, 1914, from under the cannery at Ilwaco, Wash. Ninety-four of these show the marginal band of wider rings. In all cases where the scales do not show intermediate rings the scale growth terminates in winter rings. The average size is greater than that of any other collection studied, 146.7 mm. Most of these fish were measured, a few scales were removed, and the fish were then returned to the river. The fish which were preserved were selected for unusual size. On this account data regarding the number and relative lengths of males and females are not available. The scales of these fish present no unusual features. The following table (18) contains the data:

TABLE 18.—YOUNG CHINOOKS FROM ILWACO, WASH., UNDER THE CANNERY, OCT. 24, 1914.

SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Average length.	Number—		Scale record.				Average estimated length of fish at time of formation of check.
	Total.	With check.	Average number of rings—		Average length of anterior radius—		
			To check.	Total.	To check.	Total.	
121.5 mm	6	3	7.6	21.5	24.3	61.3	49.7

SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
	Total.	With check.	Average number of rings—			Average length of anterior radius—				
			To check.	Intermediate growth.	Total.	To check.	Intermediate growth.	Total.	Check.	Intermediate growth.
201 to 205 mm	2	1	10.0	21.0	34.0	23.0	65.5	110.5	48.0	123.0
196 to 200 mm	0	0								
191 to 195 mm	2	0		18.0	31.5		58.0	108.0		110.5
186 to 190 mm	1	0		18.0	31.0		68.0	118.0		113.0
181 to 185 mm	0	0								
176 to 180 mm	2	2	8.5	19.0	31.0	28.0	60.5	93.0	53.0	115.5
171 to 175 mm	3	1	10.0	20.0	30.3	28.0	53.0	88.0	48.0	106.3
166 to 170 mm	10	3	6.3	19.1	30.0	21.3	56.5	90.3	38.0	103.5
161 to 165 mm	3	0		20.3	27.6		58.0	86.3		108.0
156 to 160 mm	6	1	12.0	18.3	26.9	48.0	57.1	87.1	88.0	103.0
151 to 155 mm	7	2	8.0	19.7	27.0	23.0	53.7	78.7	48.0	109.4
146 to 150 mm	10	6	10.0	19.4	26.4	29.6	54.0	72.0	58.2	108.0
141 to 145 mm	12	6	9.0	20.5	26.2	24.6	53.8	69.6	52.2	110.5
136 to 140 mm	12	5	7.2	20.9	27.0	24.0	53.0	72.5	46.0	101.3
131 to 135 mm	9	3	10.0	18.9	24.2	26.7	55.0	69.1	55.5	104.1
126 to 130 mm	5	2	10.0	18.8	23.2	25.7	54.6	65.0	53.0	102.0
121 to 125 mm	8	4	7.7	19.5	24.7	24.2	47.3	63.0	48.0	94.8
116 to 120 mm	1	0		20.0	22.0		56.0	63.0		98.0
111 to 115 mm	0	0								
106 to 110 mm	1	0		12.0	14.0		38.0	48.0		88.0
Total	94	36								
Average, 148.3 mm			8.6	19.5	26.6	25.8	54.6	77.2	51.3	99.9

Fifty-two specimens were taken in the McKenzie River near Leaburg, Oreg., November 2 and 3, 1915. (See Table 19.) The Oregon Fish and Game Commission maintains a hatchery here, and the fish were collected just below the point where the hatchery is located. The average length is 106.4 mm. The males, 24 in number, average 107.1 mm. in length; the 28 females, 106 mm.

A particularly interesting feature of this collection is the fact that a considerable proportion of the specimens have scales which show a distinct widening of the marginal rings. Fourteen (27 per cent) of the specimens have scales of this character. The other specimens all have scales whose marginal rings are of the narrow, winter type. The series of collections from the upper regions of the Columbia River basin is not complete enough to allow conclusions to be drawn regarding the character of this widening of the marginal rings, but it can be shown on material from the Sacramento River that the new growth of the second year usually begins during the fall. Previous to beginning this "new growth" there has been formed a more or less distinct band of narrower rings, the winter band. This is unquestionably the same phenomenon which is evident in the present case, namely, the beginning of the vigorous new growth which will continue during the growing season of the following year.

This question naturally presents itself: If this widening of the marginal rings in the case of the fish from the upper parts of the stream is to be interpreted as the new growth belonging to the second year, is it certain that the similar widening which has been found on the scales of the young fish in the estuary is not, in reality, the same thing which has merely been hastened by the migration to the brackish water in the estuary? In other words, why give different interpretations to the two phenomena?

Similar physiological causes are, in all probablity, behind the accelerated growth in each instance. The intermediate growth, however, is directly the result of changes brought about by the migration into brackish water, while the "new growth" is a response to environmental changes which are independent of any special activity on the part of the fish. The changes resulting in new growth are seasonal and affect all of the fish in any particular locality at nearly the same time of the year. The stimulus is probably not a simple one but is a complex of several factors, such as temperature, food supply, degree of maturity, etc. Racial differences in different localities may also enter as modifying factors.

The change brought about by migration is the more profound as is indicated by the fact that the rings of the intermediate growth are usually heavier and more widely spaced than those composing the new growth accomplished before migration. The difference between the two types of rapid growth is not, however, diagnostic, and it is usually impossible to distinguish in individual cases between intermediate bands and bands of new growth. Many of the fish taken in the upper part of the stream and which have begun the new growth could not be distinguished by the scales from fish taken in the estuary whose scales show the intermediate growth. From October on, therefore (and probably for some weeks previous to this time), one is likely to encounter fish in the estuary whose scales would be practically identical—having a marginal band of wider rings—but some of which will have formed the marginal band as a result of migration into brackish water, while others will have formed the marginal band in the upper parts of the stream previous to migration. Undoubtedly as the season advances the percentage of fish which have formed this band in response to the migration will decrease, while the percentage of fish which have started the new growth of the second year will increase. Since there is no method of distinguishing with certainty between the two types, the marginal band of wider rings found on the scales of the fish taken in the estuary will be referred to as the "intermediate band." In the case of fish from the upper waters, however, where the interpretation is unquestioned, we shall designate the marginal widening as "new growth."

Such a marginal band of wider rings is not always formed on the scales of fish found in the estuary. It is not apparent on the scales of the smaller migrants owing to the fact that the first few rings formed on the scales are almost always wider than those normally succeeding. They are not, however, wider than the intermediate rings but are of approximately the same width, so that no break appears at the point where the intermediate growth actually begins. The absence of the intermediate band on the scales of some of the larger migrants is probably due to the fact that those fish have not been in the brackish water long enough for the wider rings to have developed. When the intermediate growth is not found on the scales of the adult fish, which show a nuclear area of true stream growth, it probably indicates that during the seaward migration the individual did not remain long in the brackish water but continued the migration so rapidly that typical ocean rings were formed immediately succeeding typical stream rings.

The following table (19) gives the data relative to the McKenzie River collection:

TABLE 19.—YOUNG CHINOOKS FROM MCKENZIE RIVER, NOV. 2 AND 3, 1915.

SPECIMENS WITHOUT NEW GROWTH.

Length.	Number—		Scale record.				Average estimated length of fish at time of formation of check.
			Average number of rings—		Average length of anterior radius—		
	Total.	With check.	To check.	Total.	To check.	Total.	
121 to 125 mm	1	1	8.0	22.0	28.0	58.0	58.0
116 to 120 mm	1	1	7.0	19.0	28.0	58.0	63.0
111 to 115 mm	9	4	7.7	19.4	23.0	55.2	49.2
106 to 110 mm	11	8	7.7	18.7	25.5	53.0	53.5
101 to 105 mm	7	2	8.5	18.3	23.0	52.3	48.0
96 to 100 mm	6	2	8.5	17.0	23.0	48.8	45.5
91 to 95 mm	1	1	10.0	15.0	33.0	48.0	63.0
86 to 90 mm	1	1	9.0	16.0	28.0	43.0	58.0
81 to 85 mm	1	0	....	14.0	....	38.0	....
Total	38	20	....	....	....	....	....
Av. 105.8 mm	....	....	8.0	18.5	25.2	52.2	53.7

SPECIMENS WITH NEW GROWTH.

Average length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
			Average number of rings—			Average length of anterior radius—				
	Total.	With check.	To check.	In first year.	Total.	To check.	In first year.	Total.	Check.	New growth.
108.0 mm	14	5	6.6	15.7	19.8	19.0	43.4	55.5	40.0	85.1

Six young chinooks were taken at Astoria, Oreg., November 7, 1914. These were captured by hook and line from under the Union Fishermens' Cooperative Cannery. Nothing of particular interest appeared in the study of this small collection, and the table (20) is therefore presented without comment.

TABLE 20.—YOUNG CHINOOKS FROM ASTORIA, OREG., NOV. 7, 1914.

Average length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
			Average number of rings—			Average length of anterior radius—				
	Total.	With check.	To check.	To intermediate growth.	Total.	To check.	To intermediate growth.	Total.	Check.	Intermediate growth.
135.0 mm.	6	5	9.0	21.0	25.0	27.0	66.6	78.0	48.8	111.6

November 19, 1915, seven small chinooks were collected by means of a seine on a small sand bar near Warrendale, Oreg. (See Table 21.) This is on the Columbia River about 40 miles above the point where the Willamette River joins the Columbia. These fish average only 93 mm. in length, and it is worthy of note that the scales show no indication of the beginning of a period of rapid growth. The scales of one specimen show a primary check four rings from the center of the scales. Four specimens show the narrow, winter rings at the margins of the scales. The other three specimens have scales whose marginal rings are still of the summer type, no narrowing being apparent.

TABLE 21.—YOUNG CHINOOKS FROM WARRENDALE, OREG., NOV. 19, 1915.

Average length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
93 mm.	7	15	45

Scales were taken December 4, 1914, from 52 specimens of young chinooks which had been reared at the hatchery of the U. S. Bureau of Fisheries at Clackamas, Oreg. These fish were measured but not sexed. The scales of these are no exception to the rule that the scales of hatchery fish exhibit uneven and abnormal growth and are seldom of much value in scale study. Since these are fish of known age, having been reared from eggs which were spawned in the fall of 1913, it will, however, be interesting to make a comparison between them and wild fish of the same approximate age. These hatchery fish are quite irregular in their growth, so much so, in fact, as to indicate a bimodal curve. The average length is, however, about the same as the average of other collections made at the same time of year, being less than some and greater than others. The scale growth is also, in spite of its irregularities, quite comparable with that observed in the wild fish in the number and the general arrangement of the rings. The data regarding these fish are collected in the following table (22).

TABLE 22.—YOUNG CHINOOKS FROM CLACKAMAS HATCHERY, OREG., DEC. 4, 1914.

Length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
			Average number of rings—			Average length of anterior radius—				
	Total.	With check.	To check.	To— New growth.	Of— New growth.	To check.	To new growth.	Total.	Check.	New. growth.
151 to 155 mm.	1	1	6.0	23.0	2	30.0	57.0	68.0	67.0	127.0
146 to 150 mm.	2	2	8.0	24.5	2	29.0	72.0	[a] 70.0	55.5	127.0
141 to 145 mm.	0	0								
136 to 140 mm.	2	2	7.5	21.5		28.0	65.5		60.5	
131 to 135 mm.	6	6	9.3	22.0	2	28.0	68.0	81.0	54.5	115.0
126 to 130 mm.	10	9	8.5	20.1	3	28.0	57.0	70.0	56.0	110.0
121 to 125 mm.	3	3	8.3	20.6		25.5	55.5		48.0	
116 to 120 mm.	8	8	8.6	19.0		21.0	54.0		50.0	
111 to 115 mm.	12	12	8.9	19.4		24.2	55.5		51.0	
106 to 110 mm.	3	3	8.6	17.3		23.0	43.0		46.0	
101 to 105 mm.	4	4	8.2	19.4		18.0	48.0		50.5	
96 to 100 mm.	0	0								
91 to 95 mm.	1	1	10.0	17.0		23.0	53.0		43.0	
Total	52	51								
Av. 121.1 mm.			8.6	20.1	2.2	24.8	57.3	72.2	52.3	119.7

[a] The fact that this is less than the length to the beginning of the new growth is due to the fact that the specimen not having the new growth had unusually large scales.

All but nine of the specimens have winter rings at the margins of the scales. Of these, four have a marginal band of wider rings, indicating that a period of more rapid growth has begun. This is probably the new growth of the second year. The remaining five specimens still show at the margins of the scales the wide rings of the first summer's growth.

December 3 to 8, 1915, several collections were made at different points on the Columbia River between the mouth of the Willamette River and Astoria. Collecting was rather difficult on account of inclement weather and unusually high water for this time of year. Collections were made in the following places: Upper Willow Bar, Lower Willow Bar, Deer Island, Mayger, Oreg., Wallace Island, and Seal Island. Unsuccessful attempts to collect were also made at several other places. The collections are all quite small, and the total number of fish taken was but 38. This represents the results of over 30 hauls with the 100-foot seine. One of the specimens collected is a small fry only 35 mm. in length. This is obviously a fish of the year, and therefore one year younger than the other individuals. No scales have been developed. This specimen is not included with the older fish in the following table. Fourteen of the older specimens are males averaging 95.5 mm. in length. Twenty-four females average 93.4 mm. The average length of all specimens is 94 mm. No significant differences have been observed in the several collections, and they are therefore cast together in the following table (23):

TABLE 23.—YOUNG CHINOOKS FROM LOWER COLUMBIA RIVER, DEC. 3 TO 8, 1915.

SEVENTEEN SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Average length.	Scale record.	
	Average number of rings.	Average length of anterior radius.
92.3 mm	16.5	49.5

TABLE 23.—YOUNG CHINOOKS FROM LOWER COLUMBIA RIVER, DEC. 3 TO 8, 1915—Continued.

TWENTY-ONE SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at beginning of intermediate growth.
		Average number of rings—		Average length of anterior radius—		
		To intermediate growth.	Total.	To intermediate growth.	Total.	
126 to 130 mm.	1	19.0	25.0	53.0	68.0	93.0
121 to 125 mm.	0	....	....	....	....	....
116 to 120 mm.	0	....	....	....	....	....
111 to 115 mm.	1	18.0	22.0	58.0	68.0	98.0
106 to 110 mm.	3	14.7	18.7	43.0	58.0	81.3
101 to 105 mm.	1	14.0	18.0	43.0	53.0	78.0
96 to 100 mm.	4	14.5	18.5	36.7	50.5	71.7
91 to 95 mm.	1	18.0	22.0	33.0	48.0	73.0
86 to 90 mm.	4	14.2	18.2	36.7	46.7	68.0
81 to 85 mm.	5	13.5	17.5	39.0	44.0	63.0
76 to 80 mm.	1	13.0	14.0	33.0	38.0	68.0
Av. 95.1 mm.	....	14.7	18.7	38.6	50.4	72.8

Owing to the unusual severity of the winter of 1915–16, no more collections were made after the one just considered until the following March and April. The fry taken during the spring and early summer have already been considered, and it remains now to discuss the yearlings which were taken during the second year after hatching.

During the course of the seining on the lower river in March and the early part of April, 1916, a total of 47 yearlings were captured. (See p. 7.) Although these were obtained from several different localities, separate tabulation shows no special difference in the fish from different places, and the entire collection is here tabulated together. There are 26 males in the collection averaging 97.6 mm. in length and 21 females averaging 93.2 mm. The average length of the entire collection is 95.6 mm. Thirteen of the specimens do not show the wider rings at the margins of the scales, but narrow, typically winter rings. The remaining 34 specimens have the wider marginal rings which are characteristic of the young migrating fish. It has been previously indicated that the marginal band of wider rings in these yearlings which were captured in the spring are probably in large measure indicative of the new growth of the second year. The term "intermediate growth" is retained, however, for the reasons given on page 25. The following table (24) presents the data for this collection:

TABLE 24.—CHINOOK YEARLINGS FROM LOWER COLUMBIA RIVER, MAR. 31 TO APR. 2, 1916.

SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Average length.	Number—		Scale record.				Average estimated length of fish at time of formation of primary check.
	Total.	With primary check.	Average number of rings—		Average length of anterior radius—		
			To check.	Total.	To check.	Total.	
93.7 mm.	13	3	7.6	18.7	16.0	35.7	43.0

TABLE 24.—CHINOOK YEARLINGS FROM LOWER COLUMBIA RIVER, MAR. 31 TO APR. 2, 1916—Contd.

SPECIMENS WITH INTERMEDIATE GROWTH.

Length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
			Average number of rings—			Average length of anterior radius—				
	Total.	With primary check.	To primary check.	To beginning of intermediate growth.	Total.	To primary check.	To beginning of intermediate growth.	Total.	Primary check.	Intermediate growth.
111 to 115 mm	2	0	....	18.0	23.5	....	33.0	45.5	....	85.5
106 to 110 mm	0	0	....	....	....	....	....	....	....	....
101 to 105 mm	6	1	12.0	15.2	21.0	26.0	31.2	43.6	59.0	75.0
96 to 100 mm	9	0	....	16.2	19.9	....	31.2	39.9	....	78.9
91 to 95 mm	11	2	11.0	15.9	19.7	23.6	28.8	37.0	61.0	73.8
86 to 90 mm	6	1	10.0	14.8	18.9	18.0	30.0	39.0	42.0	69.5
Total	34	4	....	....	....	....	....	....	....	....
Av. 96.4 mm	....	....	11.0	15.8	20.1	23.2	30.4	39.8	55.7	75.3

April 13, 1916, collections which contained specimens of yearlings were made on Deer Island and on Cottonwood Island. The total number of yearlings in these two collections is but 22. Of these, 10 are males and 12 females. The two sexes have the same average length, 107 mm. Five specimens have scales which terminate the growth in winter rings. The scales of the remaining 17 individuals show a distinct intermediate band. The following table (25) gives the data for these collections:

TABLE 25.—CHINOOK YEARLINGS FROM DEER AND COTTONWOOD ISLANDS, APR. 13, 1916.

FIVE SPECIMENS WITHOUT INTERMEDIATE GROWTH.

Average length.	Scale record.	
	Average number of rings.	Average length of anterior radius.
110 mm	19.6	42.0

SEVENTEEN SPECIMENS WITH INTERMEDIATE GROWTH.

Average length.	Scale record.				Average estimated length of fish at beginning of intermediate growth.
	Average number of rings—		Average length of anterior radius—		
	To intermediate growth.	Total.	To intermediate growth.	Total.	
105.7 mm	15.0	17.8	34.9	42.0	87.2

A somewhat larger collection of yearlings was made May 10, 1916, at Crandall's seining ground on Grims Island. Thirty-nine specimens were taken here—16 males and 23 females. The males average 106 mm. in length, and the females 101.1 mm. All of these fish have the characteristic marginal band of wider rings on the scales. The table (26) follows:

TABLE 26.—DATA FOR 39 CHINOOK YEARLINGS FROM CRANDALL'S SEINING GROUND, ON GRIMS ISLAND, MAY 10, 1916.

Length.	Number.	Scale record.				Average estimated length of fish at beginning of intermediate growth.
		Average number of rings—		Average length of anterior radius—		
		To intermediate growth.	Total.	To intermediate growth.	Total.	
121 to 125 mm.	2	16.0	20.5	53.0	65.5	100.5
116 to 120 mm.	3	16.6	21.9	46.3	68.0	74.6
111 to 115 mm.	6	16.0	21.3	48.0	67.0	81.1
106 to 110 mm.	6	14.1	19.2	42.0	57.0	76.1
101 to 105 mm.	7	16.3	20.7	42.5	59.5	73.0
96 to 100 mm.	4	15.2	19.9	41.7	55.5	75.5
91 to 95 mm.	3	15.3	18.9	43.0	54.5	71.3
86 to 90 mm.	7	12.9	17.6	33.0	49.5	62.3
81 to 85 mm.	1	12.0	20.0	33.0	53.0	53.0
Av. 103 mm.	....	15.0	19.9	41.7	58.5	74.0

Eight specimens of yearlings were taken May 11, 1916, at Point Ellice and two at Tenasillihee Island. (See Table 27.) These are quite similar to the fish contained in the collection from Crandall's seining ground, although they average somewhat larger in size.

TABLE 27.—CHINOOK YEARLINGS FROM POINT ELLICE AND TENASILLIHEE ISLAND, MAY 11, 1916.

Average length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
			Average number of rings—			Average length of anterior radius—				
	Total.	With check.	To primary check.	To intermediate growth.	Total.	To primary check.	To intermediate growth.	Total.	Check.	Intermediate growth.
108.7 mm.	10	3	8.0	17.2	23.4	39.6	45.7	67.0	46.3	73.7

One yearling chinook was captured in the Columbia River just above the mouth of the Little White Salmon River on May 25, 1916. This specimen is a female, 98 mm. long. The scales show three rings of the new growth of the second year. The first year's growth comprises 15 rings. The anterior radius measures 45 mm. to the beginning of the new growth, and the total length is 59 mm. The estimated length at the time of beginning the new growth is 75 mm.

Fourteen yearlings were taken in the Clackamas River June 8, 1916, after which date no more yearlings were taken in any of the collections. Nine of these are males averaging 112 mm. in length. The 5 females average 112.6 mm. The scales of all these specimens show the wider rings of the new growth at the margins. The following table (28) gives the data for this collection:

TABLE 28.—CHINOOK YEARLINGS FROM CLACKAMAS RIVER, JUNE 8, 1916.

Average length.	Number—		Scale record.						Average estimated length of fish at time of formation of—	
	Total.	With check.	Average number of rings—			Average length of anterior radius—				
			To check.	To intermediate growth.	Total.	To check.	To intermediate growth.	Total.	Check.	Intermediate growth.
112.2 mm.	14	2	12.5	15.5	21.6	40.0	49.1	72.6	63.0	78.3

FISH FROM THE SACRAMENTO RIVER.

The young Sacramento River chinooks available for study may be divided into two distinct groups. The first consists of young migrants which were collected by N. B. Scofield, of the California Fish and Game Commission, in the spring of 1911. This was done during the progress of an investigation into the loss of fish resulting from the overflow of the Sacramento during the spring floods. The second group consists of collections made from the McCloud River near the hatchery of the U. S. Bureau of Fisheries at Baird, Calif. These collections were made at the request of Dr. Gilbert during 1911 and 1912. The writer is indebted to both Dr. Gilbert and Mr. Scofield for the privilege of studying these collections.

The collections of young migrants from the lower part of the Sacramento were made under quite variable conditions and in several localities. Some were made from the river proper and others from the ponds formed by the overflow of the Sacramento during the spring floods. For the most part the collections were small and in several instances were so poorly preserved that many of the specimens had lost all of the scales. Very few of the collections were well enough preserved so that the individuals could be sexed.[a]

Most of these collections comprise so few individuals that a detailed consideration of each collection would be useless. No unusual results were obtained from a separate study of these smaller collections, and therefore the totals and averages for each have been collected in the following table (29). There are included also, for the purpose of comparison, three collections of young fry from the State hatcheries at Sisson and Brookdale. The few collections which are large enough to deserve more detailed study will be considered later.

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[a] This poor preservation was in nowise the fault of the collector. The collections had been set aside as valueless several years before the writer found use for them and had received no care during the interval.

TABLE 29.—CHINOOK FRY FROM THE SACRAMENTO RIVER.

Date.	Locality.	Number.	Average length (mm.).	Scale record.	
				Average number of rings.	Average length of anterior radius.
1910. Mar. 5	Brookdale hatchery	26	36.3	(a)	(a)
1911. Mar. 8	Sisson hatchery	13	38.7	(b)	(b)
Apr. 3	do	12	41.2	(c)2.0	(c)17
Apr. 13	Sacramento River, 30 miles above Sacramento	9	57.5	4.4	23.6
Apr. 19	Cache Slough	2	67	6.0	28.2
Apr. 29	Prospect Slough	4	69	7.5	27.6
May 9	Pond near Butte Slough	13	81.5	9.2	37.5
May 15	Shag Slough	15	77	9.9	34.5
May 16	Hass Slough	4	75.2	9.5	32.2
May 27	Sausilito, Calif	8	81	10.9	37.5
May 28	Prospect Slough	16	68	7.5	28.3
June 8	Pond near Butte Slough	17	95.6	13.3	48.9
June 30	Ponds near Knights Landing, Calif	18	107.0	16.4	51.4
July 9	Pond near Butte Slough	5	92.2	14.8	47.9
1913. Jan. 4	Brookdale hatchery	55	[d]95.7	17.5	38.9

[a] No scales formed.

[b] Only a few platelets present on the largest specimens.

[c] Average of six of the largest.

[d] 15 specimens without new growth. Four specimens with new growth show: Average number of rings to new growth, 16.7; of new growth, 3.7; average length of anterior radius to new growth, 37.4; total length of anterior radius, 44.9; and average estimated length at time of beginning new growth, 92.9.

The following tables (30, 31, and 32) contain the data for those collections of wild fish which are large enough for separation into the various size groups to be of value: It was not considered necessary to present in detail the data for the collections from the Brookdale hatchery, although these are as large as many of the collections of wild fish so considered. The fry preserved March 5, 1910, have no scales and present only a slight variation in length. The series of yearlings, preserved January 4, 1913, are so variable and the scale growth is so irregular that they can not be compared in detail with the wild fish.

TABLE 30.—DATA FOR 19 FRY FROM WALNUT GROVE, CALIF., APR. 9, 1911.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
71 to 75 mm	1	8	32.2
66 to 70 mm	3	7.3	26.5
61 to 65 mm	0	....	....
56 to 60 mm	2	4.5	23.6
51 to 55 mm	2	3.5	23.6
46 to 50 mm	2	3.0	14.9
41 to 45 mm	1	1.0	14.9
36 to 40 mm	6	....	....
31 to 35 mm	2	....	....
Av. 49.0 mm	....	4.5	21.6

TABLE 31.—DATA FOR 22 FRY FROM BUTTE SLOUGH, MAY 8 AND 9, 1911.[a]

Length.	Number.
71 to 75 mm	4
66 to 70 mm	7
61 to 65 mm	5
56 to 60 mm	3
51 to 55 mm	2
46 to 50 mm	1
Av. 63.9 mm	....

[a] The specimens in this collection had all lost the scales as a result of poor preservation.

TABLE 32.—DATA FOR 20 FRY FROM POND NEAR ELKHORN, CALIF., JUNE 3, 1911.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
81 to 85 mm	4	10.2	35.4
76 to 80 mm	10	10.0	35.3
71 to 75 mm	4	9.0	34.8
66 to 70 mm	2	8.5	27.6
Av. 77.0 mm	....	9.7	34.4

This collection contained 11 males averaging 77.1 mm. in length and 9 females averaging 76.9 mm. in length.

The largest collection from the lower Sacramento River was made at Woods Break, June 5 and 6, 1911. (See Table 33.) There is a total of 147 specimens. One hundred and fifteen of these were taken in a trap located at the point where the water was flowing through the break from the main river, and 32 were seined from an overflow pond near the break. The separate study of these two collections shows no essential difference, and the data are, therefore, placed together in the following table (33). This collection, undoubtedly, is a fair sample of the migrating fry in the Sacramento at this time of year. The average length is 71.7 mm. The average number of rings on the scales is 8.2, and the average length of the anterior radius is 30.5 on the arbitrary scale adopted. There are 77 males in the collection averaging 72.2 mm. in length. The 70 females average 71.0 mm.

TABLE 33.—DATA FOR 147 FRY FROM WOODS BREAK, JUNE 5 AND 6, 1911.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
91 to 95 mm	1	11.0	48.3
86 to 90 mm	5	11.6	43.0
81 to 85 mm	14	10.1	37.2
76 to 80 mm	20	9.0	33.4
71 to 75 mm	42	8.5	31.4
66 to 70 mm	34	7.6	27.9
61 to 65 mm	24	6.8	25.8
56 to 60 mm	5	5.6	23.0
51 to 55 mm	1	4.0	20.7
46 to 50 mm	1	4.0	20.7
Av. 71.7 mm	....	8.2	30.5

A collection of 44 specimens was made at Tisdale Wier, June 24 to 26, 1911. (See Table 34.) The average length is 78.8 mm. The average number of rings on the scales is 10.3, and the length of the anterior radius is 33.1. Twenty-one males average 78 mm. and 23 females 79.6 mm. in length.

TABLE 34.—DATA FOR 44 FRY FROM TISDALE WIER, JUNE 24 TO 26, 1911.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
101 to 105 mm	1	13.0	33.0
96 to 100 mm	2	11.5	35.5
91 to 95 mm	3	12.6	34.6
86 to 90 mm	8	10.9	29.9
81 to 85 mm	6	11.0	31.5
76 to 80 mm	5	10.2	29.0
71 to 75 mm	7	10.1	27.3
66 to 70 mm	7	9.0	25.9
61 to 65 mm	4	8.5	23.0
56 to 60 mm	1	8.0	23.0
Av. 78.8 mm		10.3	33.1

This completes the description of the young fry taken in the lower Sacramento River. The skewing of the curve of length toward the smaller sizes, which was noted in the collections from the Columbia River, is not apparent in this material. It is only slightly noticeable in Tables 30 and 33. This is, at least in part, due to the fact that there are few collections of any size which contain specimens of the smallest fish. The fact that these specimens from the Sacramento were not collected in the estuary, as were most of the Columbia River fry, would doubtless also have some such effect. In the estuary the fish hesitate for a time in the brackish water before completing the migration to the ocean. This gives an opportunity for the smaller fish from above to come in and form an abnormally large proportion of the collection.

The collections from the McCloud River include two made in July and September, 1909, and a series made during the fall and winter of 1911–12. A constant feature of the collections made from July to December is the presence of precociously matured males. These also have been noted among the fish from the Columbia River basin (p. 18). Such precociously mature males will not be included in the tables with the immature fish. None of these specimens show a well-defined primary check, as was met with in the Columbia River collections.

Thirty-eight specimens were taken July 24 and 25, 1909. Nine of these are mature males and average 124 mm. in length. The scales of the mature fish have an average of 18.5 rings, and the average length of the anterior radius is 63.9. Fourteen of the immature specimens are males averaging 85.5 mm. in length and fifteen are females averaging 91.5 mm. The data for the immature specimens, 29 in number, are given in the following table (35).

TABLE 35.—DATA FOR 29 YOUNG CHINOOKS FROM MCCLOUD RIVER, BAIRD, CALIF., JULY 24 AND 25, 1909.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
111 to 115 mm	1	15.0	49.0
106 to 110 mm	1	14.0	55.0
101 to 105 mm	1	14.0	55.0
96 to 100 mm	6	13.3	51.1
91 to 95 mm	2	12.0	46.6
86 to 90 mm	6	11.3	43.7
81 to 85 mm	5	10.4	36.0
76 to 80 mm	3	9.3	36.0
71 to 75 mm	4	9.5	36.2
Av. 88.5 mm	....	11.5	43.1

A collection consisting of 82 specimens was made September 24, 1909. Seven of these are precociously mature males, averaging 109.5 mm. in length. The scales of one has a band of two wider rings at the margins. This undoubtedly represents the beginning of the new growth of the second year, since, as is presently shown, over one-half of the immature fish taken at this time have the new growth well developed. The average number of rings included within the first year's growth (extending to the periphery of the scales of all but the one specimen which shows new growth) is 15.3. The average length of the anterior radius is 43.

Seventy-five of the specimens included in this collection are immature fish, averaging 96.9 mm. in length. Forty individuals have definitely begun the new growth of the second year, as is indicated by a marginal band of wider rings. The scales of the remaining 35 individuals have marginal bands of the narrow, winter type. Thirty-two specimens are males averaging 97.9 mm. in length. Forty-three females average 96.3 mm. The data are presented in the following table (36):

TABLE 36.—YOUNG CHINOOKS FROM MCCLOUD RIVER, BAIRD, CALIF., SEPT. 24, 1909.

THIRTY-FIVE SPECIMENS WITHOUT NEW GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
121 to 125 mm	2	18.0	69.6
116 to 120 mm	0	....	....
111 to 115 mm	2	17.5	58.0
106 to 110 mm	3	16.7	49.5
101 to 105 mm	2	17.0	52.3
96 to 100 mm	6	14.3	47.5
91 to 95 mm	7	13.9	41.2
86 to 90 mm	8	13.2	40.8
81 to 85 mm	4	13.5	42.2
76 to 80 mm	0	....	....
71 to 75 mm	1	11.0	32.2
Av. 94.0 mm	....	14.5	46.0

TABLE 36.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., SEPT. 24, 1909—Continued.

FORTY SPECIMENS WITH NEW GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at beginning of new growth.
		Average number of rings—		Average length of anterior radius—		
		To new growth.	Of new growth.	To new growth.	Total.	
116 to 120 mm	1	15.0	4.0	49.5	61.0	93.0
111 to 115 mm	1	13.0	4.0	43.0	55.0	83.0
106 to 110 mm	7	13.2	3.1	43.7	56.0	86.0
101 to 105 mm	8	13.4	3.2	43.7	52.3	86.0
96 to 100 mm	13	12.9	3.3	40.3	50.2	78.0
91 to 95 mm	5	12.4	2.8	35.7	43.7	75.0
86 to 90 mm	5	11.8	2.4	36.8	44.9	73.0
Av. 99.5 mm		12.9	3.1	39.3	50.5	80.9

It is interesting to note that the scale records to the beginning of the new growth are approximately the same as the scale records of the fish which are equal in size to the estimated length at the time of beginning the new growth (80.9 mm.). Table 36 shows that the scales of fish 81 to 85 mm. in length have an average of 13.5 rings and an average length of 42.2. In the collection of specimens with new growth the average number of rings preceding the new growth is 12.9, and the average length of the anterior radius is 39.3.

September 18, 1911, 104 specimens were collected. Of these, 9 are mature males averaging 99.6 mm. in length. The scales of these males have an average of 14.2 rings, and the length of the anterior radius averages 50.7. None of the 95 immature fish had begun the new growth, the scales of all terminating in winter rings. This is in striking contrast to the condition found in 1909 when 53 per cent had started the new growth by September 24. Evidently the conditions in the same locality may vary from year to year in such a way as to materially alter the time for beginning the period of active growth. The possible results of such annual fluctuation may be of considerable importance in its effect on the future history of the fish. There are two possibilities: (1) The fish may tend to migrate earlier in those years when the new growth is started earlier; and (2) they may reach a greater size before migrating, but migrate at the same time of year. A detailed study of the fish in some one tributary extending over a series of years would be necessary to a solution to this problem. Careful attention should be paid to fluctuations in climatic conditions. Fifty-one of the immature specimens in this collection are males; 44, females. The males average 94.5 mm. in length; the females, 91.8 mm. The following table (37) presents the data regarding the immature specimens.

TABLE 37.—DATA FOR 95 YOUNG CHINOOKS FROM MCCLOUD RIVER, BAIRD, CALIF., SEPT. 18, 1911.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
106 to 110 mm.	1	17.0	61.0
101 to 105 mm.	7	15.2	51.7
96 to 100 mm.	25	14.0	49.5
91 to 95 mm.	32	13.6	45.4
86 to 90 mm.	24	12.9	42.6
81 to 85 mm.	5	11.8	36.8
76 to 80 mm.	1	11.0	38.0
Av. 93.2 mm.		13.6	46.6

The next collection was made October 18, 1911. One hundred and forty-six specimens were taken. Two of these are mature males 97 and 106 mm. in length. Their scales have an average of 15 rings, and the average length of the anterior radius is 53.2. One of the immature fish had started the new growth, as is indicated by two wider marginal rings. This specimen is 110 mm. long, and the scales have 15 rings belonging to the first year's growth. The length of the anterior radius is 36 to the end of the first year's growth and 45 to the periphery of the scales. Sixty-two males average 99.8 mm. and 81 females 98.9 mm. in length. The data for the immature fish which had not begun the new growth are given in the following table (38):

TABLE 38.—DATA FOR 143 YOUNG CHINOOKS FROM MCCLOUD RIVER, BAIRD, CALIF., OCT. 18, 1911.

SPECIMENS WITHOUT NEW GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
111 to 115 mm.	2	17.5	58.0
106 to 110 mm.	17	15.3	50.5
101 to 105 mm.	42	15.1	49.3
96 to 100 mm.	44	14.5	46.2
91 to 95 mm.	30	14.0	44.6
86 to 90 mm.	8	12.7	40.2
Av. 99.2 mm.		14.7	47.1

One hundred and thirty-six specimens were collected November 18, 1911. Six of these are mature males which average 110.5 mm. in length and whose scales have an average of 15.2 rings. The average length of the anterior radius of the scales is 53.2. Thirty-six of the remaining 130 specimens had begun the new growth of the second year. The scales of the other 94 individuals show marginal rings of the winter type. The collection contains 53 males and 77 females. The average lengths of the two sexes are the same, 101.2 mm. The table (39) follows:

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TABLE 39.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., NOV. 18, 1911.

NINETY-FOUR SPECIMENS WITHOUT NEW GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
121 to 125 mm.	2	17.5	59.8
116 to 120 mm.	1	17.0	55.0
111 to 115 mm.	2	15.5	55.2
106 to 110 mm.	15	15.3	51.1
101 to 105 mm.	27	15.3	48.9
96 to 100 mm.	35	15.0	47.1
91 to 95 mm	12	14.3	46.0
Av. 101.5 mm.		15.2	48.7

THIRTY-SIX SPECIMENS WITH NEW GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at time of beginning new growth.
		Average number of rings—		Average length of anterior radius—		
		To new growth.	Of new growth.	To new growth.	Total.	
111 to 115 mm.	1	15.0	4.0	49.0	59.0	88.0
106 to 110 mm.	8	14.6	1.8	50.0	58.0	92.5
101 to 105 mm.	7	13.4	1.8	45.4	51.2	90.1
96 to 100 mm.	14	13.4	1.8	41.4	51.4	83.0
91 to 95 mm.	5	13.0	2.0	35.7	43.7	80.0
86 to 90 mm.	1	12.0	2.0	32.2	43.0	73.0
Av. 100.5 mm.		13.7	1.9	43.1	51.8	85.9

A collection made December 18, 1916, contains 92 specimens. Only one is a mature male, 108 mm. long. The scales of this individual show 16 rings, and the length of the anterior radius is 59.8. Fifty-one (56 per cent) of the 91 immature specimens had begun the rapid growth of the new year. The average length is 101.2 mm. Forty-five males average 101.9 mm. and 46 females 100.6 mm. The table (40) follows:

TABLE 40.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., DEC. 18, 1911.

FORTY SPECIMENS WITHOUT NEW GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
116 to 120 mm.	1	18.0	55.0
111 to 115 mm.	1	17.0	49.0
106 to 110 mm.	7	16.5	53.4
101 to 105 mm.	10	15.3	50.0
96 to 100 mm.	15	14.8	46.3
91 to 95 mm.	6	15.1	46.5
86 to 90 mm.	1	13.0	38.0
Av. 100.5 mm.		15.3	48.5

TABLE 40.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., DEC. 18, 1911—Continued.

FIFTY-ONE SPECIMENS WITH NEW GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at time of beginning new growth.
		Average number of rings—		Average length of anterior radius—		
		To new growth.	Of new growth.	To new growth.	Total.	
116 to 120 mm.	1	13.0	3.0	38.0	49.0	98.0
111 to 115 mm.	3	13.6	3.0	47.1	52.0	96.3
106 to 110 mm.	5	14.4	1.8	43.7	50.6	91.0
101 to 105 mm.	20	13.6	2.0	42.0	48.3	88.5
96 to 100 mm.	17	13.3	2.1	40.6	47.4	81.2
91 to 95 mm.	5	12.4	2.0	36.8	44.8	79.0
Av. 101.7 mm.	....	13.4	2.1	40.3	48.5	86.0

January 22, 1912, 75 specimens were collected. There were no mature males among them. One of the males, however, was of unusual size, 142 mm., and the testes of this specimen were found, upon dissection, to be slightly enlarged. It is shown later (p. 68) that precociously matured males may recover from the effects of ripening the sex products, and there is no doubt that this has occurred in the individual in question. No new growth is recorded on the scales, the terminal rings being of the winter type. The large size, enlarged testes, and delayed new growth all point to the interpretation given. The scales indicate clearly that the fish was a yearling, the same age as the other specimens. They show 20 rings, and the anterior radius measures 75 on the arbitrary scale. This specimen is not included in the tables. Forty-three (58 per cent) of the other specimens had begun the new growth. Thirty-one males average 104.1 mm. in length and 43 females 102.3 mm. The table (41) follows:

TABLE 41.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., JAN. 22, 1912.

THIRTY-ONE SPECIMENS WITHOUT NEW GROWTH.

Length.	Number.	Scale record.	
		Average number of rings.	Average length of anterior radius.
111 to 115 mm.	5	16.6	55.1
106 to 110 mm.	2	16.5	49.5
101 to 105 mm.	11	15.7	51.0
96 to 100 mm.	7	14.7	48.5
91 to 95 mm.	5	14.6	46.0
86 to 90 mm.	1	14.0	38.0
Av. 101.7 mm.	....	15.5	49.9

TABLE 41.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., JAN. 22, 1912—Continued.

FORTY-THREE SPECIMENS WITH NEW GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at time of beginning new growth.
		Average number of rings—		Average length of anterior radius—		
		To new growth.	Of new growth.	To new growth.	Total.	
111 to 115 mm.	6	13.7	3.5	44.3	55.2	90.5
106 to 110 mm.	11	13.3	2.7	44.9	55.8	90.0
101 to 105 mm.	13	13.2	2.6	40.2	49.5	85.5
96 to 100 mm.	12	12.9	2.7	39.7	49.5	81.5
91 to 95 mm.	1	11.0	3.0	32.0	43.0	73.0
Av. 104.0 mm.		13.2	2.8	41.5	51.7	86.0

February 27, 1912, 26 specimens were taken. One is a mature male, 127 mm. long. The scales of this individual show 18 rings in the first year's growth and 1 in the second year's growth. The length of the anterior radius is 51 to the beginning of the new growth and 57 to the periphery of the scale. The estimated length at the time of beginning the new growth is 114 mm. Twelve of the immature specimens show the new growth at the margins of the scales. The other 13 specimens terminate the scale growth in winter rings. The average length of the entire collection is 111.6 mm. Twelve males average 110.9 mm. in length; 13 females, 112.2 mm. The table (42) follows:

TABLE 42.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., FEB. 27, 1912.

THIRTEEN SPECIMENS WITHOUT NEW GROWTH.

Average length.	Scale record.	
	Average number of rings.	Average length of anterior radius.
109.2 mm.	16.9	52.2

TWELVE SPECIMENS WITH NEW GROWTH.

Average length.	Scale record.				Average estimated length of fish at time of beginning new growth.
	Average number of rings—		Average length of anterior radius—		
	To new growth.	Of new growth.	To new growth.	Total.	
114.2 mm.	15.6	2.4	48.0	56.5	95.9

The last collection from Baird was made March 2, 1912. This contains 31 specimens averaging 109.6 mm. in length. There are no mature fish. Twelve males average 110.5 mm. and 19 females 109 mm. in length. Twenty-two (71 per cent) had begun the new growth. The table (43) follows:

TABLE 43.—YOUNG CHINOOKS FROM McCLOUD RIVER, BAIRD, CALIF., MAR. 2, 1912.

NINE SPECIMENS WITHOUT NEW GROWTH.

Average length.	Scale record.	
	Average number of rings.	Average length of anterior radius.
105.8 mm	16.4	50.7

TWENTY-TWO SPECIMENS WITH NEW GROWTH.

Length.	Number.	Scale record.				Average estimated length of fish at time of beginning new growth.
		Average number of rings—		Average length of anterior radius—		
		To new growth.	Of new growth.	To new growth.	Total.	
121 to 125 mm	2	16.0	3.0	49.5	61.0	98.0
116 to 120 mm	1	17.0	2.0	49.0	55.0	103.0
111 to 115 mm	9	15.9	2.3	47.5	55.8	97.0
106 to 110 mm	7	15.1	2.1	48.5	57.0	93.5
101 to 105 mm	3	13.7	2.3	41.4	53.3	84.5
Av. 111.2 mm		15.4	2.5	47.3	56.2	94.8

MISCELLANEOUS COLLECTIONS.

With but two exceptions the miscellaneous collections were made by Prof. J. O. Snyder, of Stanford University, during the progress of biological investigations of the coastal streams of California and Oregon carried on during the summers of 1897 and 1899. One of the exceptions referred to is a collection, consisting of but three specimens, which was made by the writer in 1915 at Hope Island, Puget Sound, Wash. The other exception is one specimen which was collected in the ocean at Half Moon Bay, Calif., some 20 miles south of the mouth of the Sacramento River.

The collections from the coastal streams are for the most part small, and a detailed consideration of each collection will be unnecessary. Measurements of the scales were not made. The data are presented in the following table (44):

TABLE 44.—MISCELLANEOUS COLLECTIONS OF YOUNG CHINOOKS FROM COASTAL STREAMS OF CALIFORNIA AND OREGON.

Date.	Locality.	Length (mm.).	Number.			Scale record.		
						Number of rings—		
			Total.	With primary check.	With migratory check.	To primary check.	To migratory check.	Total.
1897. July 6	Bear River, Calif., not far from the mouth.	76 to 80	4	0	4	....	9.5	14.5
		71 to 75	11	0	6	....	8.5	12.9
		66 to 70	8	0	5	....	7.4	11.5
		61 to 65	3	0	2	....	7.5	12.0
		56 to 60	3	0	1	....	8.0	12.3
Total	....	....	29	0	18	....	....	....
Average	....	69.5	....	....	....	....	8.3	12.6
July 8	Little River, Calif., from mouth up about 500 yards.	81 to 85	2	0	2	....	9.0	14.5
		76 to 80	3	0	3	....	8.6	12.6
		71 to 75	9	0	7	....	6.8	11.9
		66 to 70	9	0	9	....	7.5	11.9
		61 to 65	1	0	1	....	7.0	11.0
Total	....	....	24	0	22	....	....	....
Average	....	72.1	....	....	....	....	7.6	12.2
July 19	Deer Creek, Oreg., 40 miles from the mouth.	[a] 68.0	7	6	....	[a] 6.8	....	[a] 11.0
July 24	Shasta River, Calif., tributary to the Klamath River.	[a] 75.8	[b] 6	5	....	[a] 9.8	....	[a] 13.5
1899. July 30	Flores Creek, Oreg., near tidewater.	76 to 80	1	0	0	....	....	14.0
		71 to 75	6	0	5	....	10.0	13.8
		66 to 70	12	0	4	....	8.2	13.3
		61 to 65	8	0	2	....	7.0	13.1
		56 to 60	3	0	0	....	....	11.0
Total	....	....	30	0	11	....	....	....
Average	....	67.0	....	....	....	....	8.8	13.2
Aug. 5	Elk Creek, Curry County, Oreg., near tidewater.	91 to 95	2	0	1	....	8.0	17.5
		86 to 90	3	0	3	....	10.6	18.0
		81 to 85	4	0	2	....	10.5	14.5
		76 to 80	12	0	12	....	10.4	14.2
		71 to 75	4	0	4	....	8.5	13.7
		66 to 70	2	0	1	....	11.0	13.0
Total	....	....	27	0	23	....	....	....
Average	....	79.5	....	....	....	....	10.0	14.8
Aug. 6	Sixes River, Oreg., near tidewater.	[a] 77.6	6	0	2	....	[a] 10.5	[a] 15.0
Sept. 6	Siletz River, Oreg., about 20 miles above mouth.	[a] 93.2	4	0	3	....	[a] 7.0	[a] 17.5
Sept. 14	Nestucca River, Oreg., 10 miles above mouth.	[a] 115.5	4	3	4	[a] 3.6	[a] 15.0	[a] 21.2
Sept. 15	Trask River, Oreg., just above tidewater.	[a] 91.5	13	0	7	....	[a] 15.2	[a] 18.5
Sept. 16	Nehalem River, Oreg., just ahead of incoming tide.	[a] 104.0	19	0	19	....	[a] 15.8	[a] 20.5

[a] Average. [b] Two mature males.

The fish contained in these collections are obviously all fry, hatched from eggs laid down during the fall previous to the date of capture. No striking variation in size is noticeable, other than that which is apparently dependent on greater age, those fish collected later in the year averaging somewhat larger. The same uniformity is characteristic of the scale growth. A more detailed study of much larger collections might, however, discover special characteristics of growth or of scale record in the different streams. The primary check appears in only one of the collections which were made close to tidewater, the one from the Nestucca River. The check observed on the scales of the specimens from Shasta River and Deer Creek (collected toward the headwaters of these streams) is undoubtedly the same as the primary check noted in upstream fish from the Columbia River basin. (See p. 18.) A band of intermediate rings is characteristic of varying proportions of the fish contained in all of the collections made near tidewater and is in every respect similar to the intermediate growth of the Columbia River migrants. Although the available data are meager, it seems safe to state that the history of the fish in these smaller streams is, in its general aspects, similar to the history of young fish collected in the Columbia River at the same time of year.

The three specimens taken near Hope Island, Puget Sound, were the only chinooks among some 70 specimens captured by hook and line in one of the fish traps located at this point. The remaining specimens were yearling silver salmon averaging about 100 mm. in length. There is no means of knowing whether this is the normal proportion existing between young silvers and young chinooks in this part of the sound at this time of year. It may be that the young chinooks do not lead into the traps as readily as the silvers; or they may be less willing to take the hook. These three chinooks were, respectively, 130, 97, and 94 mm. in length. All were males. On examining the scales it was surprising to find that, in spite of the negligible difference in size between the two smaller fish, the smallest individual was a fry and the two larger ones both yearlings. The record on the scales is perfectly clear, leaving no doubt as to the proper interpretation. The scales of the two smaller individuals, differing but 3 mm. in length, are reproduced in Plate IV, figures 6 and 7. The scales of the smallest individual show no indication of stream growth, and there is no doubt that this fish migrated as a young fry and that the scales represent a purely ocean type of nucleus in the process of formation. The scales of the fry show 13 rings, and the length of the anterior radius is 50. The scales of the smaller yearling have 13 rings to the end of the first year's growth and 5 in the intermediate growth. Those of the larger yearling have 19 rings to the end of the first year and 8 in the intermediate band. The scale measurements are as follows: 130 mm. specimen, 55 to beginning of the intermediate growth, total, 92; 97 mm. specimen, 28 to intermediate growth, total, 47.

The young chinook from Half Moon Bay, Calif., is of particular interest, since it is, so far as the author knows, the smallest individual which has been captured in the open ocean at any distance from the mouth of the parent stream. Unfortunately, there are no data as to the date of capture, except that it was previous to 1913. The specimen presumably came from the Sacramento River, since at the time this was captured no chinooks were known to spawn in the streams south of San Francisco.[a] This fish was approximately 100 mm. long. The scales (Pl. IV, fig. 8) indicate clearly a period of life spent in the stream followed by a sharply demarked area representing ocean growth. That part of the scale indicative of stream growth is precisely similar to the scales of young migrating fish taken in the spring and summer on the lower Sacramento River (Pl. III, fig. 6).

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[a] Within the past six or seven years a run of chinook salmon has been established in the San Lorenzo River, Santa Cruz Co., Calif., by the late Supt. F. A. Shebley, of the California Fish and Game Commission.

CONCLUSIONS.

RATE OF GROWTH.

An analysis of the data from the Columbia River shows that all of the collections are not strictly comparable, since the rate of growth is markedly variable in different parts of the river. The environmental conditions in different regions of the watershed are so variable that this is not surprising. Therefore the collections have been separated into four groups, each group having been taken under approximately similar conditions. These four groups are as follows: (1) From the main river above the estuary (the estuary is considered as that part of the river below Tenasillihee Island, about 18 miles above Astoria); (2) from the estuary exclusive of the collections made under the canneries; (3) from under canneries in the estuary; (4) from Clackamas hatchery and the Clackamas River near the hatchery. In addition, there are the collections from the Little White Salmon River, from the McKenzie River, and from the lake at Seufert, Oreg.; but these are not included in this grouping.

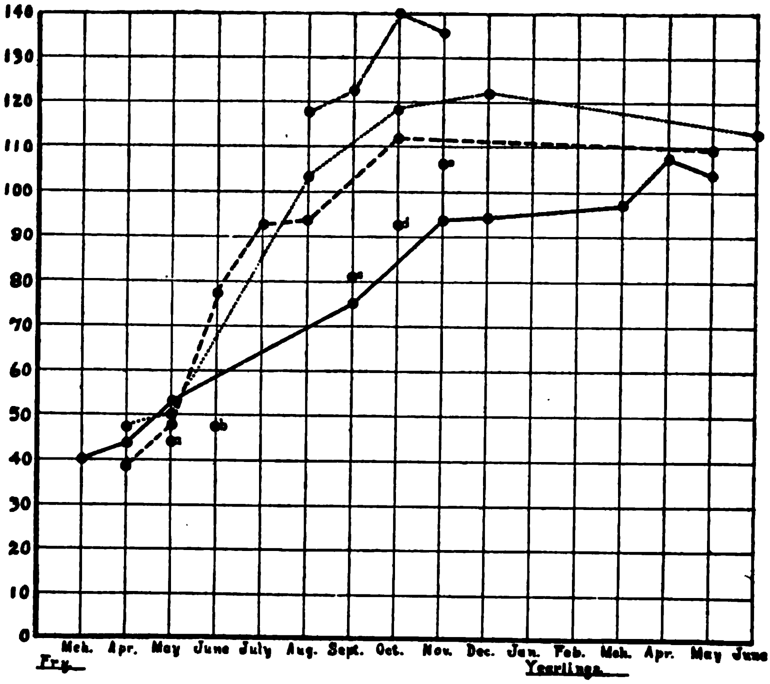
In the following table (45) the data which have been previously presented in separate tables are recombined, so as to show the average lengths, during each month of the year, of the fish captured in each of the four divisions of the river and in the Little White Salmon and McKenzie Rivers. These same data, with the addition of those for the collection from the lake at Seufert, Oreg., are presented in graph 1. In the graph, however, the collections from the mouth of the small creek near Point Ellice and from the Columbia River near the mouth of Little White Salmon River have been kept separate.

TABLE 45.—AVERAGE LENGTH OF SPECIMENS FROM THE COLUMBIA RIVER FOR EACH MONTH.

Month.	Group 1.		Group 2.		Group 3.		Group 4.	
	Locality.	Length.	Locality.	Length.	Locality.	Length.	Locality.	Length.
FRY.		*Mm.*		*Mm.*		*Mm.*		*Mm.*
March	Grims Island	40.0						
April	Cottonwood and Deer Islands.	43.2	Several points in estuary.	38.1			Clackamas hatchery.	46.5
May	Crandall's seining ground.	52.5	do	47.3			do	49.5
	Near mouth of Little White Salmon River.	44.6						
June			Small creek near Point Ellice.	47.7				
			Other points in estuary.	77.0				
July			Point Ellice	92.2				
August			do	94.0	Ilwaco, Wash	118.0	Clackamas River.	112.9
September	Crandall's seining ground.	74.5			do	122.0		
October			Point Ellice	112.7	Astoria, Oreg	127.5	Clackamas River.	118.0
					Ilwaco, Wash	146.7	[Little White Salmon River.	92.5]
November	Warrendale, Oreg	93.0			Astoria, Oreg	135.0	[McKenzie River.	105.8]
December	Several points on the lower river.	93.9					Clackamas hatchery.	121.1
YEARLINGS.								
March	do	95.9						
April	Cottonwood and Deer Islands.	107.0						
May	Crandall's seining ground.	103.0	Point Ellice and Tenasillihee Island.	108.7				
June							Clackamas River.	112.2

One of the most striking features of the growth as shown by this tabulation is the constant difference in average size maintained in different parts of the stream.

The smallest fish taken are those comprising group 1, from the main river above the estuary. The rate of increase in the size of these fish is quite regular, although there is a period from November until March when the growth is practically negligible. In April and May a second period of rapid growth is apparently started, although more data collected during subsequent months would be necessary to prove this. Since no yearlings are found in the river after June, it is impossible to get this information.



GRAPH 1.—Rate of growth of young chinook salmon from different regions of the Columbia River Basin. Figures at left of graph indicate length of fish in mm.; solid line, group 1; broken line, group 2; dots and dashes, group 3; dotted line, group 4; *a*, Columbia River near mouth of Little White Salmon River; *b*, small creek near Point Ellice; *c*, lake at Seufert, Oreg.; *d*, Little White Salmon River; and *e*, McKenzie River.

Until after May there is no particular difference in the size of the fry from different portions of the stream. However, in later collections it is seen that those composing group 1 are smallest, followed, in the order of increasing size, by those of group 2 (from the estuary), group 4 (from the Clackamas River), and group 3 (from under the canneries at Ilwaco and Astoria).

The greater size of the fish of group 2 as compared with those of group 1 is undoubtedly due to the more rapid rate of growth maintained in the estuary. In the same manner the greater size of the fish taken from under the canneries is due to the more rapid rate of growth of those fish which acquire the habit of feeding on the abundant offal. The fact that fish taken under canneries are so uniformly different from those taken but a short distance away indicates that the young salmon congregate at these points and that individuals may remain here for some time feeding heavily on the offal and as a consequence growing with unusual rapidity. The greater size of the fish from the Clackamas River, as compared with those of groups 1 and 2, may be due to a racial difference characteristic of the fish in this tributary or to the fact that many of these fish have, in all probability, been reared for a part or all of their lives in the hatchery.

The rate of growth in the estuary, and especially under the canneries at Ilwaco and Astoria, is distinctly more rapid than in the higher waters. The increase in length is especially rapid during June, July, and August, by which time the fry in the estuary have far outstripped those in the upper part of the stream—in fact, have reached a greater size than will be attained during the remainder of the year by those individuals that do not migrate early. The growth in the estuary during September and October is positive, but much slower than that which took place during the three months just preceding. After the month of October the data pertaining to fish from the estuary is very scanty, but apparently a period during which little or no growth takes place follows, this coinciding with a similar condition in the regions upstream.

It will be noted on the graph that the final tendency of each of the curves is downward. This seems conclusive evidence that the larger individuals migrate earlier. Gilbert (1915) has found this to be true of young, seaward migrants of the sockeye salmon. The present author's conclusion that the young fish in the tributary streams tend to migrate shortly after beginning the new growth, if not before, also indicates that the larger specimens migrate earlier, since it has also been shown that the specimens which have begun the new growth invariably average larger than those which have not done so.

The single collections from Seufert, Little White Salmon River, and the McKenzie River do not offer any basis for estimation of the actual rate of growth during successive months, but it will be seen that they agree in general with the growth of fish in the main river, averaging somewhat more than the fish in group 1, but less than those of group 2.

In the case of fish taken from the Columbia River proper it may not be strictly correct to speak of the increasing size as growth. In all probability fish that have once entered the main river continue, more or less steadily, their migration to the ocean. We would thus be dealing, in successive months, with entirely different lots of fish. In a general way, however, our figures should show the main features of the growth.

At the time the fry become free swimming they are between 35 and 40 mm. in length. During March, April, and May the average length does not exceed 50 mm. Above the estuary the growth is quite regular from the time the fry first appear until October or November, by which time an average length of between 90 and 100 mm. has been attained. For the next several months no particular growth is recorded. The collections of yearlings made in April and May from the Clackamas River indicate that a new period of growth has been initiated, but because of the fact that about this time the last of the fish leave the tributary on their downward migration no further data are available. The rate of growth as indicated by these data has undoubtedly been modified by the migration of part of the fish. As has been shown, the larger fish tend to migrate earlier than the smaller ones. This would tend to slow up the growth curve and to obscure the sharp rise during the early summer so conspicuous for the curves for the other groups.

It has been shown that new growth is recorded on the scales of fish in tributary streams as early as October or November (p. 25). Since there is no conspicuous increase in the amount of new growth between this time and the following May or June, and since, also, it has been shown that the fish entering the estuary during the late fall or winter may show a marginal band identical with the "new growth" observed in the tributaries, it seems safe to conclude that the young fish start the downward migration soon after beginning the new growth, if not before. This matter is given further consideration in the sections dealing with scale development and with migration.

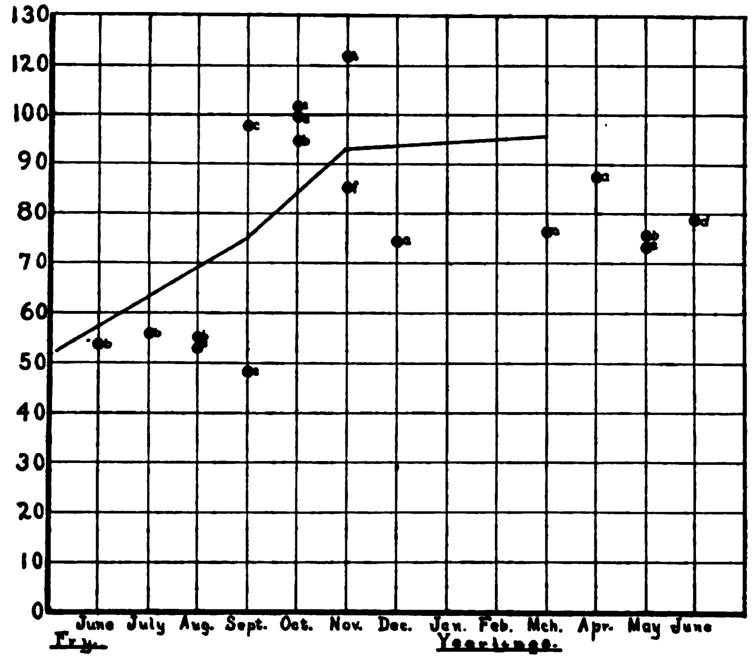
The estimated size at the time of beginning the new, or the intermediate, growth is given in the following table (46) and in graph 2. (Consideration of the collection made at Seufert, which has already been discussed, and of the one made at the Clackamas hatchery in December, 1914, is omitted here.)

TABLE 46.—AVERAGE ESTIMATED LENGTH AT TIME OF BEGINNING NEW GROWTH (GROUP 4) OR INTERMEDIATE GROWTH (GROUPS 1, 2, AND 3).

Month.	Group 1.		Group 2.		Group 3.		Group 4.	
	Locality.	Length.	Locality.	Length.	Locality.	Length.	Locality.	Length.
FRY.		*Mm.*		*Mm.*		*Mm.*		*Mm.*
June			Estuary, except from small creek near Point Ellice.	53.3				
July			Point Ellice	55.3				
August			do	54.5	Ilwaco	54.0		
September					do	97.5		
October			Point Ellice	94.7	Ilwaco and Astoria.	101.9	Clackamas River.	99.3
November					Astoria	111.6	[McKenzie River.	85.1]
December	Several points on lower Columbia.	73.7						
YEARLINGS.								
March	do	75.2						
April	Cottonwood and Deer Islands.	87.3						
May	Crandall's	74.0	Point Ellice and Tenasillihee Island.	74.8				
June							Clackamas River	78.3

There is a distinct grouping of the estimated lengths at the time of beginning the intermediate growth about three modes, as follows: During June, July, and August the mode is approximately 55 mm.; during September, October, and November, approximately 100 mm.; and during the remainder of the time in which the young are taken in the river, approximately 80 mm. This may be an accidental result due to insufficient data; but it is believed that there is something fundamental concerned. The mode at 55 mm. agrees fairly well with the length of the young chinooks planted in the pond at Seufert. (See p. 18.) It seems probable, therefore, that the check from which this estimate was made represents some incident in the early history of the fry comparable with the transfer from hatchery to more natural conditions. Therefore, this estimated length may represent either the size at the time of planting from the hatcheries, the size at the time the fish left the smaller streams on their downward migration, or the size at the time of entering the brackish water of the estuary. The mode at 80 mm. represents the size attained at the time of beginning the new growth of the second year.

This is shown by the close correspondence in estimated size of the yearlings at the time of beginning the more rapid growth of the second year. This correspondence also indicates that the yearlings migrating in the spring are a homogeneous lot and that the check preceding the intermediate growth (in Groups 1 and 2) is the same as that preceding the new growth (in Group 4); that is, that this check in both instances is in reality the winter band. (See discussion on p. 57.) The mode at 100 mm. undoubtedly represents, in the fall migrants, the size at the time of entering the estuary. It is possible that these differences in the estimated size at which the intermediate growth begins may be of value in determining, from the adult scales, the time at which migration took place.



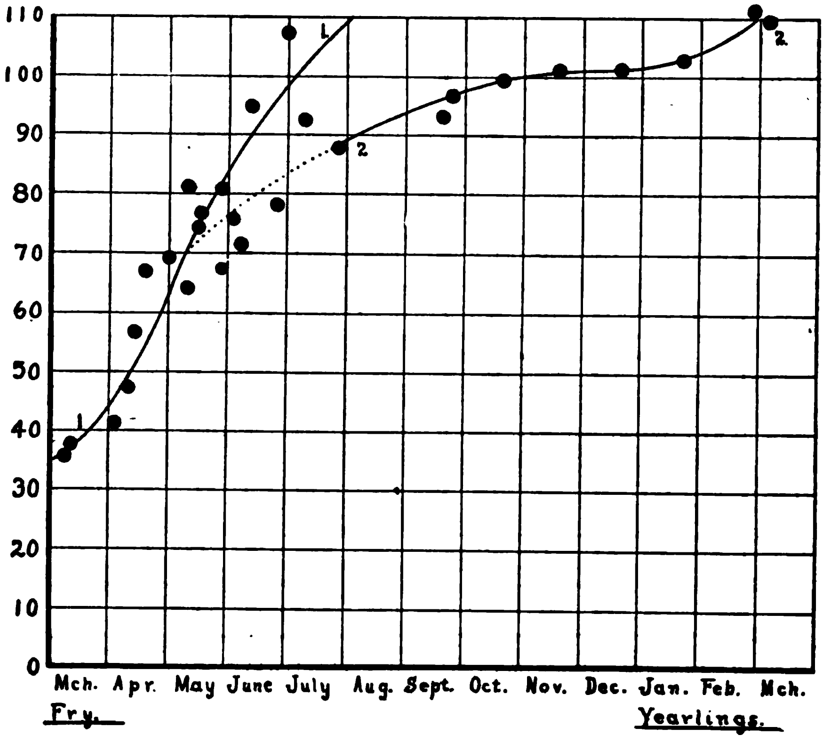
GRAPH 2.—Estimated length at time of beginning intermediate growth (groups 1, 2, and 3) and new growth (group 4). Figures at left of graph indicate length of fish in mm.; *a*, group 1; *b*, group 2; *c*, group 3; *d*, group 4; *e*, creek at Seufert, Oreg.; *f*, McKenzie River; and solid line, growth curve for group 1 (from fig. 1).

The rate of growth of the migrating fry in the Sacramento River is given in Table 47 and is shown in graph 3.

TABLE 47.—MIGRATING FRY FROM SACRAMENTO RIVER.

Date.	Locality.	Length.	Date.	Locality.	Length.
		Mm.			*Mm.*
Mar. 5	Brookdale	36.3	May 15	Shag Slough	77.0
Mar. 8	Sisson	38.7	May 16	Hass Slough	75.2
Apr. 3	do	41.2	May 27	Sausalito	81.0
Apr. 9	Walnut Grove	48.1	May 28	Prospect Slough	68.0
Apr. 13	Sacramento River 30 miles above Sacramento.	57.5	June 3	Elkhorn	76.8
			June 5 and 6	Woods Break	71.0
Apr. 19	Cache Slough	67.0	June 8	Pond near Butte Slough	95.6
Apr. 29	Prospect Slough	69.0	June 24 to 26	Tisdale wier	78.8
May 8 and 9	Butte Slough	64.1	June 30	Ponds near Knights Landing	107.0
May 9	Pond near Butte Slough	81.5	July 9	Pond near Butte Slough	92.2

The average length of the fry at the time of hatching is the same as for the Columbia River fish, 35 to 40 mm. The data here presented give only the earlier part of the growth. The rapid rise of the curve during April, May, and June is conspicuous. In comparison with the rate of growth in the Columbia River it is seen that, while the rate itself is approximately the same, the time at which the most rapid growth takes place is fully a month earlier. This is, in all probability, due to the fact that, as a whole, the water in the Sacramento Basin is warmer than that in the Columbia River Basin. As a consequence, the eggs hatch sooner and the growth is somewhat more rapid.



GRAPH 3.—Rate of growth of young chinook salmon in the Sacramento River Basin. Figures at left of graph indicate length of fish in mm.; dotted line represents probable growth of McCloud River fish, May to July; 1, lower part of river; 2; McCloud River.

The rate of growth in the McCloud River is shown in the following statement and in graph 3.

GROWTH OF YOUNG CHINOOKS IN McCLOUD RIVER AT BAIRD.	Length, Mm.
July 24, 1909	88.5
September 24, 1909	96.9
September 18, 1911	93.2
October 18, 1911	99.2
November 18, 1911	101.3
December 18, 1911	101.2
January 22, 1912	103.0
February 27, 1912	111.6
March 2, 1912	109.6

There is here merely the upper end of a curve of growth which began in the early months of the year, when the fry were 35 to 40 mm. in length. The earlier part of the curve is undoubtedly represented quite accurately by the data obtained from the collections from the lower part of the river.

In graph 3 the lines give a generalized curve combining the data from the two regions of the Sacramento. The dotted line represents the probable growth of McCloud River fish during May, June, and July. This curve represents approximately the normal rate of growth in the Sacramento Basin. It is interesting to note that the indications are quite clear that the growth of the migrating fish does not slow up during June and July, as is the case with the fish from the McCloud River. It is more than likely that the yearlings in the McCloud River would begin to show the slower growth in May if data were available.

The single collections from the coastal streams offer no basis for the analysis of growth. The collections from the Siletz, Trask, Nehalem, and Nestucca Rivers average about the same as those taken at the same time of year from the Sacramento and Columbia Rivers. The rate of growth in these streams is, therefore, probably about the same as in the larger rivers. The collections from the Bear, Little, Shasta, and Sixes Rivers and from Deer, Flores, and Elk Creeks average smaller in size than the collections from the Sacramento and Columbia Rivers. It may be concluded that the rate of growth in these streams is slower than in the others studied. Any conclusions, however, based on such scanty material must necessarily be merely tentative.

It may be stated in a general way that the growth of young chinook salmon in fresh water is most rapid during the first three or four months after the appearance of the fry. The time of year during which this rapid growth takes place varies in different streams, according to the time at which the fry make their appearance. The prevailing temperature of the water is also an important factor. After this first period of rapid growth the rate rapidly decreases during another period of about three months, until finally growth practically ceases for the year. A new period of rapid growth is apparently begun during the early months of the second year in case the fish remain in fresh water.

At the time the yolk sac is absorbed and the fry become free-swimming the average length is between 35 and 40 mm. By the end of the first period of most active growth a length of 80 or 90 mm. has been attained. The average length attained during the entire first year is approximately 100 mm.

The effect of migration into the brackish water of the estuary is to decidedly stimulate the growth.

DEVELOPMENT OF SCALES.

This section, dealing with the development of the scales, is, in certain respects, the most important part of this study. The work on the young fish was undertaken primarily, as has been previously mentioned, in order to supply an established basis for the interpretation of the nuclear portion of the adult scales. The especial need was data sufficient to permit a reasonably accurate determination, from the adult scales, of the time of migration. To this end are recorded here in detail the data bearing both on ring counts and the length of the anterior radii. The data for the Columbia River fish are given in Table 48 and in graphs 4 to 7.

TABLE 48.—FISH FROM THE COLUMBIA RIVER: AVERAGE LENGTH AND SCALE DEVELOPMENT FOR EACH MONTH.

GROUP 1.

Month.	Locality.	Specimens.			Scale record.			
		Length.	With scales with rings.	With new or intermediate growth.	Number of rings—		Length of anterior radius—	
					To beginning of rapid growth.	Total.	To beginning of rapid growth.	Total.
FRY.		Mm.	Per cent.	Per cent.				
March	Grims Island	40.0	38.0	0.0	....	1.4	....	7.0
April	Cottonwood and Deer Islands	43.2	96.0	.0	....	3.3	....	17.1
May	Crandall's seining ground	52.5	88.0	.0	....	4.9	....	22.4
	Near the mouth of Little White Salmon River	44.6	78.0	.0	....	3.1	....	26.5
September	Crandall's	74.5	100.0	5.0	(a)	13.1	....	40.1
					[b] 7.0	16.0	21.3	47.3
November	Warrendale	93.0	100.0	.0	....	15.0	....	45.0
December	Several points on the lower river	93.9	100.0	55.0	(a)	16.5	....	49.5
					[b] 14.7	18.7	38.6	50.4
YEARLINGS.								
March	Several points on the lower river	95.9	100.0	72.0	(c)	18.7	....	35.7
					[d] 15.8	20.0	30.3	39.8
April	Cottonwood and Deer Islands	107.0	100.0	77.0	(c)	19.6	....	42.0
					[d] 15.0	17.8	34.9	41.0
May	Crandall's	103.0	100.0	100.0	15.0	19.9	41.7	58.5

GROUP 2.

FRY.								
April	Several points in estuary	38.0	13.0	0.0	....	1.7	....	6.3
May	.....do	47.3	86.0	.0	....	4.2	....	20.6
June	Small creek near Point Ellice	47.7	97.0	.0	....	4.1	....	20.5
	Other points in estuary	77.0	100.0	17.0	(c)	9.5	....	38.1
					[d] 11.6	16.2	26.7	42.4
July	Point Ellice	92.2	100.0	70.0	(c)	11.9	....	46.4
					[d] 7.6	13.1	28.5	49.8
August	.....do	93.9	100.0	58.0	(c)	13.5	....	45.7
					[d] 8.5	16.1	28.2	52.3
October	.....do	112.7	100.0	24.0	(c)	22.1	....	59.8
					[d] 20.3	23.4	50.7	60.6
YEARLINGS.								
May	Point Ellice and Tenasillihee Island	108.7	100.0	100.0	17.2	23.4	45.7	67.0

GROUP 3.

FRY.								
August	Ilwaco	118.0	100.0	0.0	....	21.3	....	61.3
September	.....do	123.0	100.0	80.0	(c)	20.2	....	59.4
					[d] 17.2	22.4	48.1	62.0
October	Astoria	127.5	100.0	70.0	(c)	23.2	....	64.5
					[d] 21.8	26.0	58.0	73.0
	Ilwaco	146.7	100.0	94.0	(c)	21.5	....	61.3
					[d] 19.5	26.6	54.6	77.1
November	Astoria	135.0	100.0	84.0	(c)	33.0	....	73.0
					[d] 18.6	22.6	65.4	78.0

[a] Without new growth.
[b] With new growth.

[c] Without intermediate growth.
[d] With intermediate growth.

TABLE 48.—FISH FROM THE COLUMBIA RIVER: AVERAGE LENGTH AND SCALE DEVELOPMENT FOR EACH MONTH—Continued.

GROUP 4.

Month.	Locality.	Specimens.			Scale record.			
		Length.	With scales with rings.	With new or intermediate growth.	Number of rings—		Length of anterior radius—	
					To beginning of rapid growth.	Total.	To beginning of rapid growth.	Total.
FRY.		Mm.	Per cent.	Per cent.				
April	Clackamas hatchery	46.5	100.0	0.0		5.4		18.8
May	do	49.5	100.0	0.0		5.9		29.1
August	Clackamas River	112.9	100.0	0.0		20.7		58.2
October	do	118.0	100.0	14.0	(a)	20.6		64.6
					[b] 20.0	25.0	58.0	77.0
	Little White Salmon River [c]	92.5	100.0	0.0		15.8		52.5
November	McKenzie River [c]	106.4	100.0	27.0	(a)	18.5		52.2
					[b] 15.7	19.8	43.4	55.5
December	Clackamas hatchery	121.1	100.0	8.0	(a)	20.0		56.0
					[b] 21.7	24.0	62.7	73.0
YEARLINGS.								
June	Clackamas River	112.2	100.0	100.0	15.5	21.6	49.1	72.6

[a] Without new growth.
[b] With new growth.
[c] These collections are given with the Clackamas series for the purpose of comparison.

The chief generalizations derived from the data recorded here are:

1. The increase in the number of rings on the scales and the increase in the length of the anterior radii are proportionate to the increase in length of the fish.

2. Hatchery-reared fish develop scales with rings earlier than do wild fish.

3. The length of those fish whose scales show a marginal band of wider rings (intermediate or new growth) is usually greater than that of fish taken at the same time and place, but whose scales do not present such a marginal band. As a corollary to this, the length of the scales and the total number of rings are greater in those fish which have started a period of active growth than in those, taken at the same time, which have not done so.

4. The number of rings in the intermediate band (or the band of new growth in Group 4) and the width of this band are somewhat greater in the spring yearling migrants than in the fall fry migrants.

5. This increase in the size of the intermediate (or new) band is not due to an increase in the size of the fish, which is not apparent, but to the fact that the part of the scales central to the beginning of the intermediate band is smaller in the spring than in the fall fish. This indicates that the fall migrants are larger before beginning the intermediate growth than are the spring migrants and is indicative of the earlier migration of the larger fish noted elsewhere.

6. In collections which contain both specimens whose scales show the intermediate growth and those which do not, the number of rings and the length of the anterior radius are less to the beginning of the intermediate growth than to the periphery of the scales on which such growth is not present. Since the fish which have not begun the intermediate growth have, in all probability, entered the estuary more recently than those

which have begun such growth, this would seem to indicate that the later migrants reach actually a greater size before migrating than do the earlier migrants. It is possible, however, that the scales are larger proportionately in the later migrants, the fish themselves being the same size, or even smaller. In such a large river as the Columbia, where the young migrants are coming from numerous tributaries, such generalizations require careful confirmation.

The author has been unable to see any systematic arrangement in the occurrence of the primary check. The cause of the formation of such a check has been traced in the collection from Seufert; but it is not to be inferred that the change from the hatchery environment to one approximating normal, wild conditions is the only cause behind the formation of such a check. Other somewhat similar environmental changes early in the life of the fish would undoubtedly result in a similar check.

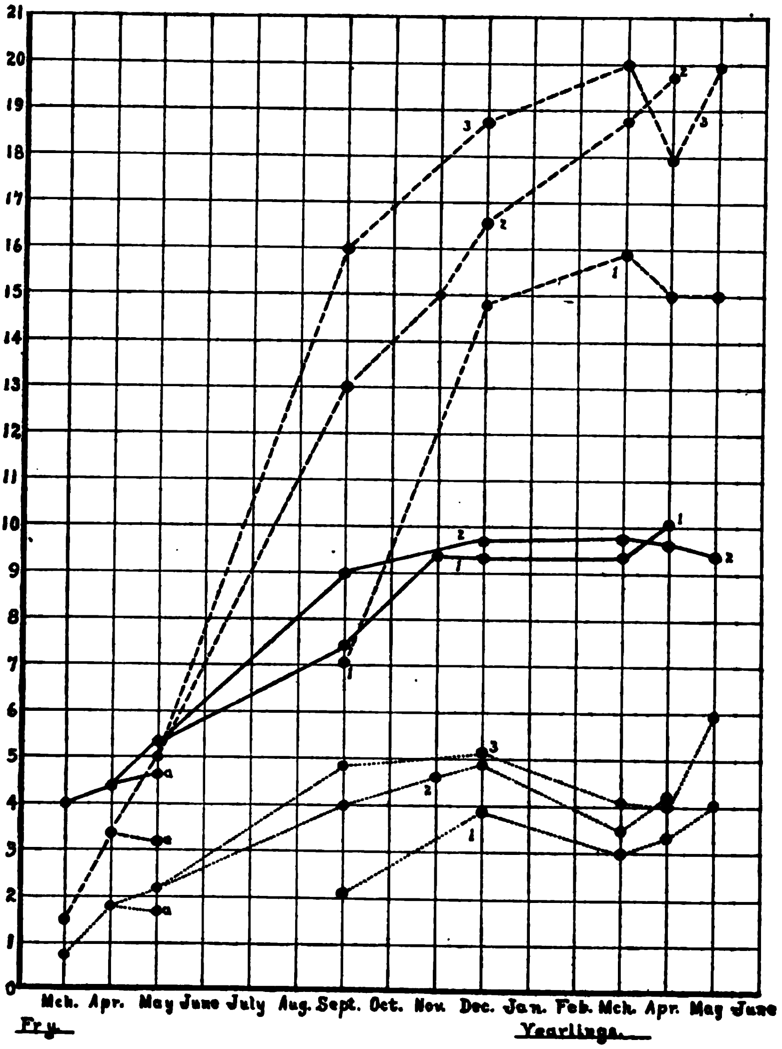
In Table 49 are presented in percentages the data regarding the type of marginal rings found on the scales during successive months on the Columbia River. During the early months the marginal rings of the fry are always of the summer type [type (1) in the table]; that is, are not conspicuously narrowed. In August is encountered the first development of narrow, winter rings [type (2)], and from this time on until April varying proportions of the specimens have marginal rings of this type. After the time when the marginal winter rings begin to be a feature of the scale growth it may be expected that the intermediate band, when formed, will be preceded, in some instances, at least, by a distinct band of narrower rings. After the winter bands begin to appear there is a constantly decreasing percentage of specimens whose scales show marginal rings belonging to the growth of the first summer in fresh water.

TABLE 49.—PERCENTAGE OF FISH WHOSE SCALES SHOW MARGINAL RINGS OF (1) SUMMER TYPE NOT ASSOCIATED WITH INTERMEDIATE OR NEW GROWTH, (2) WINTER TYPE, (3) SUMMER RINGS OF NEW OR INTERMEDIATE GROWTH.

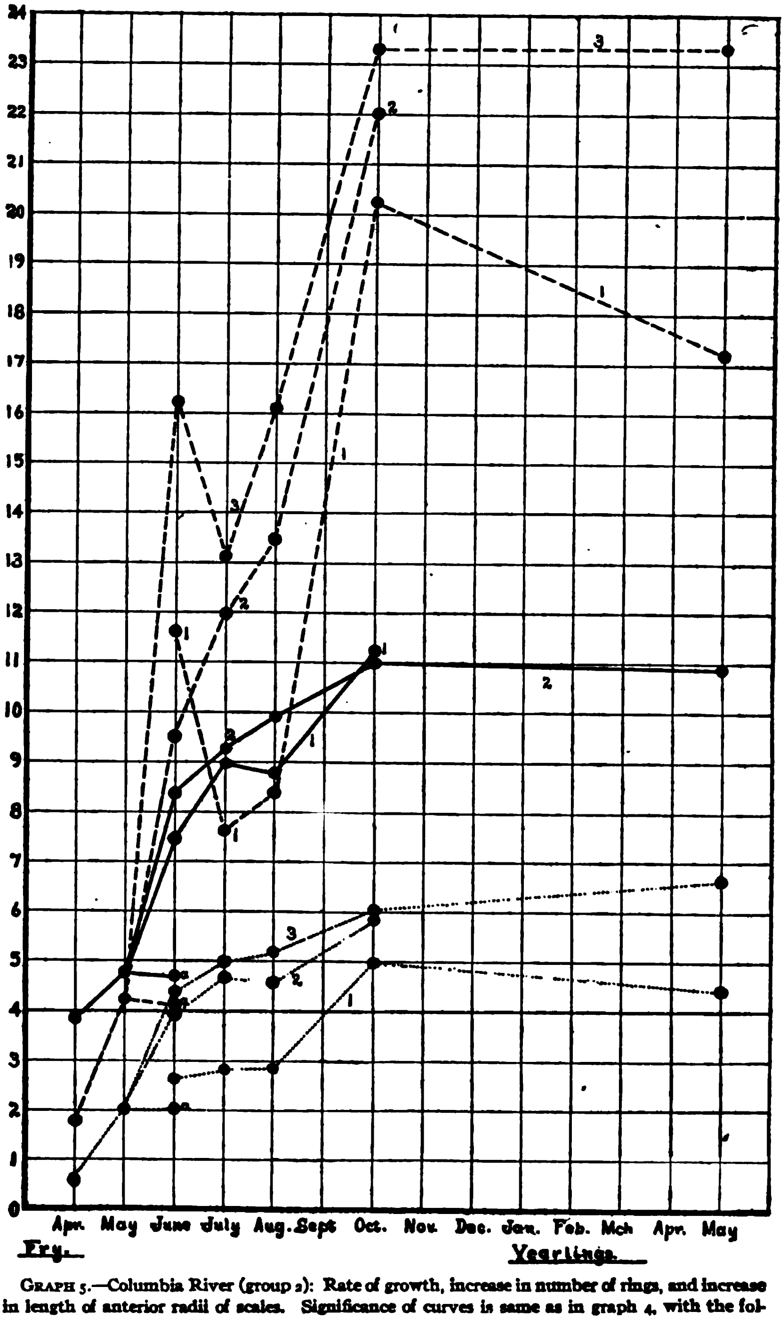
Month.	Group 1.			Group 2.			Group 3.			Group 4.		
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)
FRY.												
March	100	0	0	......	......	......	......	......	......	......	......	......
April	100	0	0	100	0	0	......	......	......	100	0	0
May	100	0	0	100	0	0	......	......	......	100	0	0
June	......	......	......	83	0	17	......	......	......	......	......	......
July	......	......	......	30	0	70	......	......	......	......	......	......
August	......	......	......	40	2	58	0	67	33	20	80	0
September	21	74	5	......	......	......	6	14	80	[a] 65	35	0
October	[b] 100	0	0	0	76	24	0	15	85	0	86	14
November	[a] 43	57	0	......	......	......	0	16	84	[d] 25	48	27
December	0	45	55	......	......	......	......	......	......	[e] 9	83	8
YEARLINGS.												
March	0	28	72	......	......	......	......	......	......	......	......	......
April	0	23	77	......	......	......	......	......	......	......	......	......
May	0	0	100	0	0	100	......	......	......	......	......	......
June	......	......	......	......	......	......	......	......	......	0	0	100

[a] Seufert.
[b] Little White Salmon River.
[c] Warrendale.
[d] McKenzie River.
[e] Clackamas hatchery.

With the exception of the collection from Clackamas hatchery none of the fish taken after November shows marginal rings belonging to the first summer's growth. Such changes as these, combined with the development of an intermediate band, will result



GRAPH 4.—Columbia River (group 1): Rate of growth, increase in number of rings, and increase in length of anterior radii of scales. Figures at left of graph indicate ordinate values for the three types of curves, as follows: (1) For curve of length, *centimeters;* (2) for number of rings, *ordinary numerical values;* (3) for length of anterior radii, *arbitrary units* (*actual value, 0.00834 mm.*). Solid line indicates length of—1, specimens without intermediate growth; and 2, specimens with intermediate growth. Broken line indicates number of rings on the scales—1, to intermediate growth; 2, total for specimens without intermediate growth; and 3, total for specimens with intermediate growth. Dotted line indicates length of anterior radii—1, to intermediate growth; 2, total for specimens without intermediate growth: and 3, total for specimens with intermediate growth. *a* indicates collection from Columbia River near mouth of Little White Salmon River.

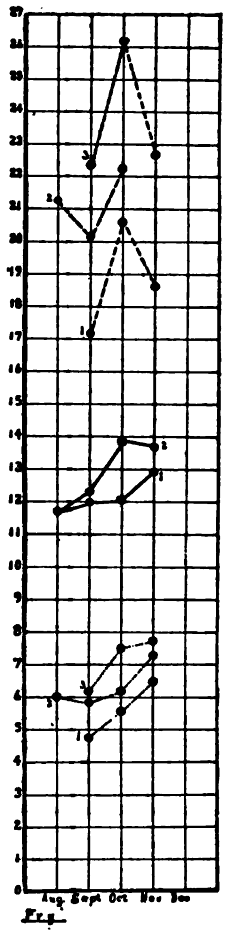


GRAPH 5.—Columbia River (group 2): Rate of growth, increase in number of rings, and increase in length of anterior radii of scales. Significance of curves is same as in graph 4, with the following exception: *a* indicates collection from mouth of small creek near Point Ellice.

in a constantly increasing percentage of fish whose scales show an intermediate band preceded by a band of distinctly narrowed rings. The fry migrating in August and September will contain a relatively small percentage of specimens whose scales are of this type. As the season advances this percentage gradually increases, as the percentage of fish entering the estuary from above and having begun the slower winter growth, increases. When fish which have not begun the slower growth enter the estuary, the vigorous intermediate growth may begin immediately, so that no distinctly narrow rings will intervene between the growth of the first summer and the intermediate growth. All possible gradations between these two types of scales may be seen among the fall migrants. The migrating yearlings taken in the spring all have the band of narrow winter rings preceding the intermediate growth.

The question arises: Is there any criterion whereby fry migrating seaward in the fall and yearlings migrating seaward in the spring can be distinguished? It has been shown that there is an average difference in the following respects: (1) Spring yearling migrants show a larger average amount of intermediate growth, both on the basis of ring counts and scale measurements; and (2) the intermediate band in the case of fall migrants is less frequently preceded by a band of narrower rings. Although these average differences in the scale growth of the fall fry and the spring yearling migrants are well enough established they are not diagnostic, and it would be impossible in many cases to determine from the scales the time at which migration took place.

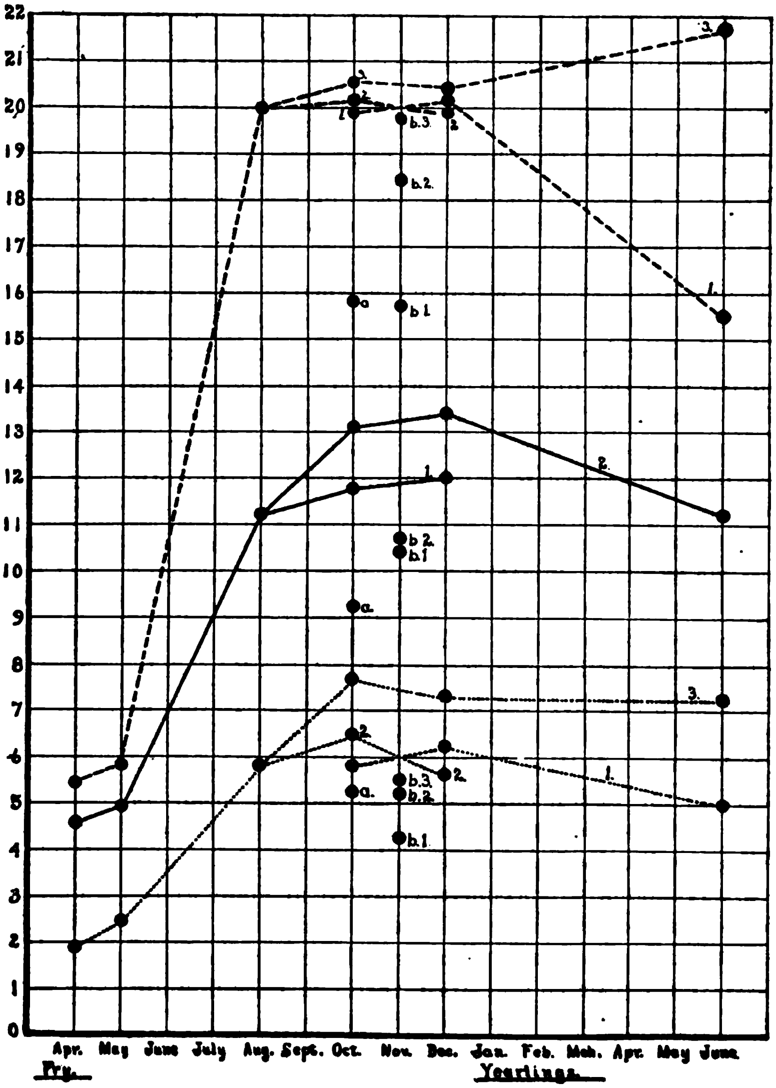
Owing to the practical importance of determining, if possible, any discernible difference between the scales of fish migrating at such widely separated times, a series of each group was photographed in order to see whether some criterion, independent of the data presented in the tables, might be established by means of which the fish could be identified. The necessity for such series of photographs was discussed on page 6. For this purpose there were selected, at random, 50 specimens collected at Point Ellice, October 16, 1915, as representative of the fall migrants, and 50 specimens of the spring, yearling migrants collected on the lower Columbia River during March and April, 1916. A careful study of these series of photographs has disclosed no such criterion as was sought, and the conclusion is forced that, so far as the nuclear growth alone is concerned, it can not be hoped to distinguish in all cases adult fish which have migrated as fry in the fall from those which have migrated as yearlings in the spring. Plate II, figures 1 to 4, and Plate III, figures 1 to 4, were selected from these photographs as examples of the scales of the fall and spring migrants.



GRAPH 6.—Columbia River (group 3): Rate of growth, increase in number of rings, and increase in length of anterior radii of scales. Significance of curves is same as in graph 4.

The available data regarding the scale growth of the Sacramento River fish do not indicate that there is as much variation as has been shown to exist in the case of the

Columbia River fry and yearlings. With the exception of the three earliest collections, made at hatcheries, all of the fish possess scales with rings. Very few of the wild fish taken on the lower river show the marginal band of wider rings, the intermediate band, which is so characteristic of the young migrants on the Columbia River. This may be accounted for by the fact that none of these collections from the Sacramento was made in San Francisco Bay, which corresponds to the estuary of the Columbia, where intermediate growth was found most commonly. The collections of yearlings made at Brookdale and the majority of the collections made in the McCloud River contain



GRAPH 7.—Columbia River (group 4): Rate of growth, increase in number of rings, and increase in length of anterior radii of scales. Significance of curves is same as in graph 4, with the following exceptions: *a* indicates collection from Little White Salmon River; *b*, collection from McKenzie River; and "new growth" takes the place of "intermediate growth."

specimens whose scales show the marginal band of wider rings indicative of the new growth of the second year.

The "primary check" which has been noted on the scales of the Columbia River fish does not appear conspicuously in the Sacramento series. In the case of the fish from the lower part of the river this is not surprising, since such a primary check has not been found on the scales of specimens from the lower part of the Columbia until autumn, considerably later in the year than the last collection from the lower Sacramento. The absence of the primary check in the collections from the McCloud may well be a racial characteristic, just as the presence of such a check is a racial characteristic of the young fish in the McKenzie River. (Compare Pl. I, fig. 8, a scale from one of the McKenzie River fish, with Pl. III, fig. 9, a scale from one of the McCloud River specimens.)

Table 50 gives the data, averaged for each month, for the collections from the lower part of the river. Table 51 gives the data for the collections from the McCloud River. Graph 8 gives the data regarding scale growth based on all the available data from the Sacramento River system. In this graph the line representing the growth of the fish is the same as the generalized curve developed in graph 3.

TABLE 50.—RATE OF GROWTH AND SCALE DEVELOPMENT IN LOWER SACRAMENTO RIVER.

Month.	Length.	Average number of rings.	Average length of anterior radii.
	Mm.		
March	37.2	....	....
April	50.8	4.5	22.3
May	72.7	9.1	33.7
June	77.3	9.6	34.1
July	92.2	14.8	47.9

TABLE 51.—McCLOUD RIVER: AVERAGE LENGTH AND SCALE DEVELOPMENT FOR EACH MONTH.

Month.	Specimens.		Scale record.			
			Number of rings—		Length of anterior radius—	
	Length.	With new growth.	To beginning of new growth.	Total.	To beginning of new growth.	Total.
FRY.	*Mm.*	*Per cent.*				
July	83.5	0.0	....	11.5	....	43.1
September:						
1909	96.9	53.0	(a)	14.5	....	46.0
			[b] 12.9	16.0	39.3	50.5
1911	93.3	0.0	....	13.6	....	46.6
October	99.2	0.7	(a)	14.6	....	47.1
			[b] 15.0	17.0	36.0	45.0
November	101.3	28.0	(a)	15.2	....	48.7
			[b] 13.7	15.6	43.1	51.8
December	101.2	56.0	(a)	15.3	....	48.5
			[b] 13.4	15.5	40.3	48.5
YEARLINGS.						
January	103.0	58.0	(a)	15.5	....	49.9
			[b] 13.2	16.0	41.5	51.7
February	111.6	48.0	(a)	16.9	....	52.2
			[b] 15.6	18.0	48.0	56.5
March	109.6	71.0	(a)	16.4	....	50.7
			[b] 15.4	17.9	47.3	56.2

[a] Without new growth.

[b] With new growth.

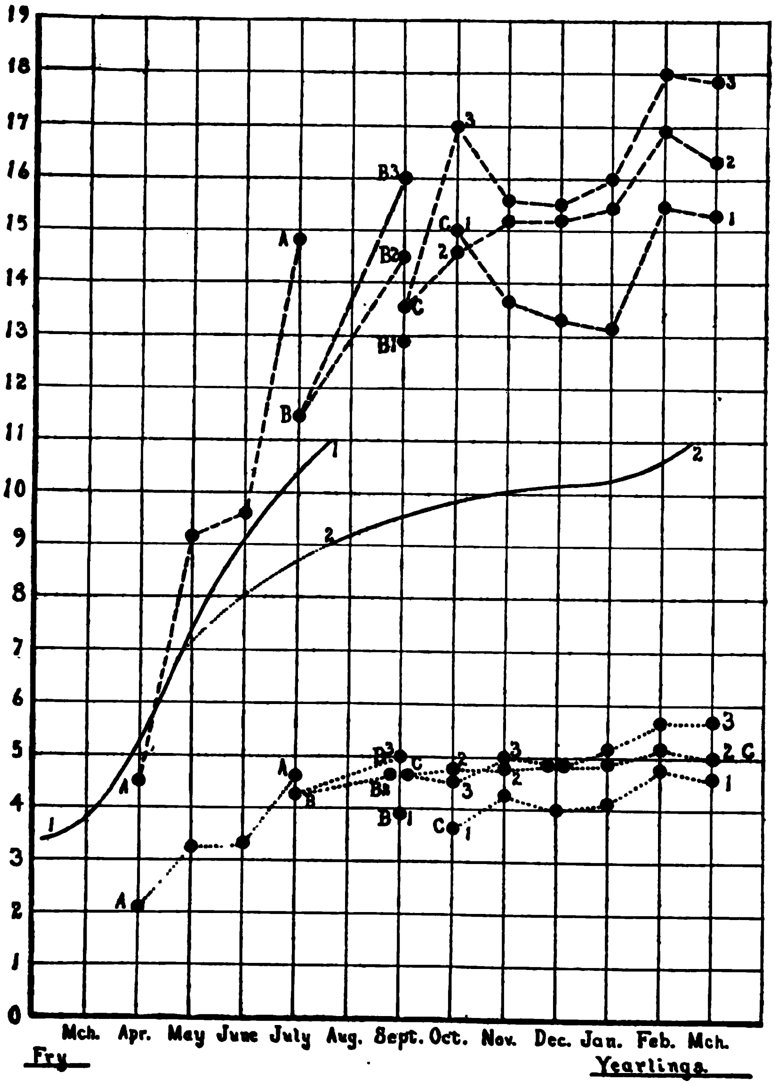
Tables 50 and 51 and graph 8 show that, as in the case of the rate of growth, the general features of scale development are not conspicuously different in the Sacramento River from those found in the Columbia River. As a result of the earlier beginning of the growth (noted on p. 50) the scale development also starts earlier.

So far as can be judged by the available data, none of the fry migrating in the spring will show a distinct narrowing preceding the intermediate growth. Inasmuch as the water of the Sacramento River becomes so warm during the summer that young salmon can not survive in it, it seems probable that the collections studied represent quite completely the migrating fry, and therefore it may be concluded that few, if any, of these will show a band of narrow rings preceding the intermediate band. There is very little evidence to show when the yearlings migrate, if at all, or whether there is any migration of fry during the late fall or winter. It would be logical to expect to find that fish older than the fry migrating in their first spring do migrate, and it seems probable that many, if not all, of such older migrants would show a band of narrower winter rings preceding the intermediate band. The evidence for this is given in Table 52, in which it is seen that none of the fish taken later than August has scales whose marginal rings belong to the first summer's growth. None of the fry collected in the lower part of the Sacramento shows scales whose marginal rings are of the winter type. There have been entered, therefore, in the following table (52) only the data on the collections from the McCloud River:

TABLE 52.—PERCENTAGE OF FISH FROM McCLOUD RIVER WHOSE SCALES SHOW MARGINAL RINGS OF (1) SUMMER TYPE BELONGING TO THE FIRST SUMMER'S GROWTH, (2) WINTER TYPE, (3) SUMMER RINGS OF NEW OR INTERMEDIATE GROWTH, ASSOCIATED WITH THE SECOND PERIOD OF RAPID GROWTH.

Month.	(1)	(2)	(3)
FRY.			
1909:			
July	45.0	55.0	0.0
September	.0	47.0	53.0
1911:			
September	.0	100.0	.0
October	.0	99.3	.7
November	.0	72.0	28.0
December	.0	44.0	56.0
YEARLINGS.			
1912:			
January	.0	42.0	58.0
February	.0	52.0	48.0
March	.0	29.0	71.0

If the author's supposition is correct that there is a migration of older fish sharply separated from the spring migration of fry, it would be expected that there would be two distinct types of nuclei found on the scales of the adults—one characteristic of fish which had migrated as fry in the spring and which shows no particular narrowing preceding the intermediate or ocean growth, and the other type showing a narrowing preceding the intermediate or ocean growth representative of fish which had migrated either in the fall as fry or as yearlings in the spring. A more detailed study of the young migrants in the Sacramento, involving collections made throughout the year, would be necessary to firmly establish this hypothesis. The spring and fall runs of adult fish in the Sacramento River are sharply separated, and a study of the scales of adults belonging to these two runs would seem to offer interesting possibilities.



GRAPH 8.—Sacramento River: Rate of growth, increase in number of rings on scales, and increase in length of anterior radii of scales. Significance of curves is same as in graph 4, with the following exceptions: Solid line indicates the generalized curve of length developed on graph 3. Broken line indicates number of rings on scales—1, to beginning of new growth; 2, total for specimens not showing new growth; and 3, total for specimens showing new growth. Dotted line indicates length of anterior radii—1, to beginning of new growth; 2, total for specimens not showing new growth; and 3, total for specimens showing new growth. A indicates collections from lower part of river; B, McCloud River, 1909; and C, McCloud River, 1911–12.

The scale growth of the fish from the coastal streams presents nothing unusual or of particular value because of the scarcity of data. Certain racial characters are suggested by the data from one or two of the streams, but the evidence does not warrant drawing even tentative conclusions.

MIGRATION.

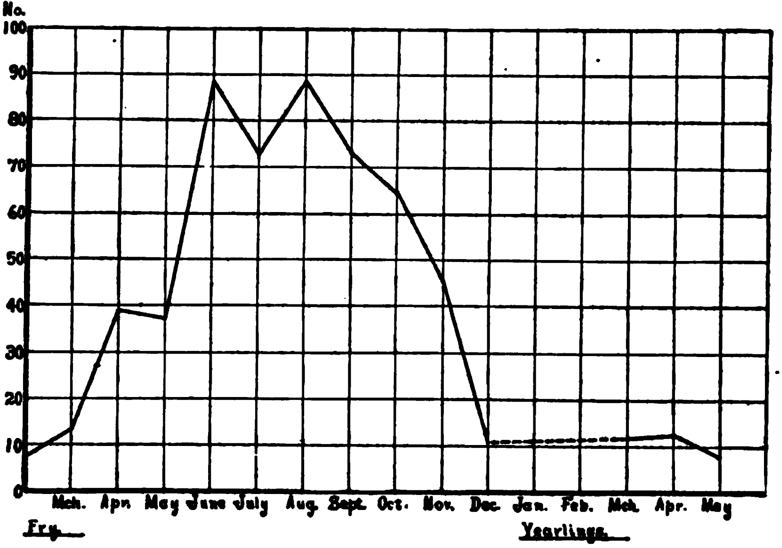
In the preceding sections the matter of migration has been dealt with in only a general way, and an attempt will now be made to summarize the available facts.

In the Columbia River migration takes place throughout the year. The fry hatched during the fall and winter may migrate immediately after the yolk sac is absorbed or even before this process is entirely completed, since occasionally specimens which still retained part of the yolk have been found in the estuary. The earliest hatched fry may migrate as early as December, and by March the migration is well under way. The data regarding the time at which the greater proportion migrate are not especially satisfactory, as the accurate determination of this would involve collecting either with some form of stationary gear or by frequent and uniform hauls with a seine at some one point. Such collecting would need to be continued during each month of the year. The nearest approach that can be made with the present data to a determination of the time of most frequent migration is by finding the average number of fish contained in each collection made in the lower part of the main river (exclusive of the collections made under canneries). This method is subject to considerable error, especially owing to the fact that at the times when the young fish were relatively scarce the collecting was more persistent and more seine hauls were made, on the average, at each point where collections were made, in order to get as large a representation of the migrants as possible. Obviously, such a source of error will tend to broaden the mean time of migration over more time than is actually the case. The data are presented in Table 53. The process of "smoothing," by which the figures in the fifth column were obtained, is the one commonly used. The smoothed figure for each month is obtained by taking the average of the actual figures for the month in question, plus those for both thc preceding and succeeding months. Graph 9 gives the smoothed curve.

TABLE 53.—COLUMBIA RIVER: AVERAGE NUMBER OF FISH IN EACH COLLECTION.

Month.	Number of specimens.	Number of collections.	Average number of specimens to each collection.	Preceding column smoothed.
FRY.				
March	102	4	25.2	19.1
April	26	2	13.0	39.4
May	321	4	80.2	37.8
June	80	3	20.2	89.0
July	166	1	166.0	72.6
August	64	2	32.0	89.0
September	69	1	69.0	73.3
October	119	1	119.0	65.0
November	7	1	7.0	46.6
December	38	3	12.6	10.6
YEARLINGS.				
March	47	4	12.0	11.9
April	22	2	11.0	12.3
May	57	4	14.0	12.2

As stated above, migration in the Columbia River takes place throughout the year, but the data here presented indicate clearly that the chief period of migration for the fry is during the months from June to October, inclusive. On account of the source of error mentioned above it seems probable that the main period of migration is actually somewhat shorter than is here indicated. The mode of the curve, showing the height of the migration, would not necessarily be affected by error of this sort. The migration of yearlings is completed by June. This wide range in the time of migration is not surprising in such a large river system as that of the Columbia, where a great diversity of climatic conditions obtains in different regions. There are two possible explanations for the wide extension of the migration period: (1) Fish from each tributary may migrate gradually, a few at a time, through the year; (2) fish from each tributary may all migrate at about the same time, but migration from different tributaries takes place at different times of the year.



GRAPH 9.—"Smoothed" curve showing average number of specimens taken in each collection in the main Columbia River and the estuary for each month.

There is some evidence to show that the young fish from particular tributaries tend to migrate at the same time and, moreover, that they tend to school together during the seaward migration. The collection made at Crandall's seining ground, September 15, 1916, especially suggests this interpretation, as the fish are noticeably smaller and the character of the scale growth different from other collections made during the same time of year under approximately similar conditions. (See p. 19.)

The time at which the fry leave the tributary streams for the main river and the rate of downward migration have not been determined. Undoubtedly, the time of leaving the tributary streams is subject to great variation. On purely a priori grounds it seems certain that the earliest fry to migrate—such, for example, as those taken in March and April—must have come from the lower tributaries. The spawning season in the different tributaries does not differ more than a few weeks over the entire Columbia system, but the much colder water of the higher streams delays development so markedly that there may be a difference of several months in the time at which the yolk sac will be fully absorbed and the fish begin an active existence. It can not well be doubted, then, that the earliest fry to migrate have been hatched in the lower tributaries, and it seems reasonable to assume that, in a general way, at least, the successively later migrants have come from successively higher tributaries.

The abnormally large proportion of smaller fish found in the lower part of the river during the spring and early summer, which causes the "skewing" of the frequency curve of length noted on page 8, may also indicate that the height of the migration has not been passed and that the smaller fish entering from above are doing so in constantly increasing numbers. After the height of the migration the skewing effect of the constantly decreasing numbers of smaller fish would not be noticeable. This skewing of the curves of length is not found to any noticeable degree after the early part of the summer, a fact which seems to give additional evidence that the height of migration comes, in the lower part of the Columbia River, during the latter half of the summer or early in autumn.

The migration of fry in the Sacramento River has been given in detail by Rutter (1903). He found that fry were migrating in the lower part of the river during the months from January to May, inclusive, and that they started the migration from the streams in which they were hatched as soon as the yolk sac was absorbed, as early as October. This migration is much earlier than that observed by the author in the Columbia River, a fact associated with the earlier hatching of the eggs and the more rapid development of the fry in the warmer water of the southern stream. The data presented in this study add nothing to Rutter's conclusions on this point. No migrating yearlings were taken by Rutter (1903) nor by Scofield (1898) in their work on the lower river, but, as no collections were made during the fall and early winter, it is quite possible that there is a migration of the older fish at this time of the year. It is possible that yearlings migrating in the spring are so scarce that none were captured. It has been shown (p. 36) that the new growth of the second year may begin in the case of the young chinooks in the McCloud River as early as September, varying, however, in different years. It has also been shown (p. 48) that in some cases, at least, there is a tendency for the older fry or yearlings to migrate soon after beginning the new growth of the second year. Consideration of these two facts lends considerable probability to the theory that there is a fall migration of older fry in the Sacramento River. An investigation of this matter would be pertinent, since a distinct difference in the scale growth between fry migrating in the spring and those migrating in the fall would be expected. The relation between the young migrating at these two periods (granting that such a later migration takes place) and the adults comprising the sharply separated spring and fall runs of spawning fish might well prove to be of considerable practical importance.

VARIATIONS DUE TO SEX.

SEX PROPORTIONS.

The proportions of males and females in the collections from the Columbia River, while subject to considerable variation in different collections, are on the whole remarkably even. The data for each collection are presented in Table 54. There seems to be no regularity to the variations noted, and the conclusion that males and females migrate seaward in equal numbers throughout the year seems justified.

TABLE 54.—COLUMBIA RIVER: PROPORTION OF MALES AND FEMALES, AVERAGE LENGTH OF MALES AND FEMALES, AND LENGTH OF FEMALES AS PERCENTAGE OF THE LENGTH OF MALES.

Date.	Locality.	Males.		Females.		
		Percentage.	Length in millimeters.	Percentage.	Length—	
					In millimeters.	As percentage of the male length.
FRY.						
1916:						
Apr. 13	Cottonwood and Deer Islands	50	42.3	50	44.1	104
May 2	Clackamas hatchery	53	46.5	47	46.9	101
May 10	Lower Columbia	54	52.3	46	52.8	101
May 11	Estuary	50	46.7	50	48.8	105
May 25	Columbia River near Little White Salmon River	50	44.6	50	44.6	100
May 27	Clackamas hatchery	50	53.0	50	59.0	111
June 13	Small creek near Point Ellice	53	47.5	47	48.0	101
Do	Estuary	44	78.5	56	74.9	95
July 19	Point Ellice	46	90.1	54	93.6	104
Aug. 12	do	62	92.0	38	97.2	106
Aug. 30 and 31	Clackamas River	50	113.8	50	112.0	99
1915:						
Sept. 2	Seufert	48	81.5	52	80.3	99
1916:						
Sept. 15	Crandall's	52	74.2	48	74.8	101
1914:						
Sept. 17	Ilwaco	51	121.3	49	124.7	102
1915:						
Oct. 16	Point Ellice	51	112.2	49	113.3	101
Oct. 17	Astoria	54	127.9	46	127.0	99+
Nov. 2 and 3	McKenzie River	46	107.1	54	106.0	99
Dec. 3 to 8	Lower Columbia	37	95.5	63	93.4	98
YEARLINGS.						
1916:						
Mar. 31 to Apr. 2	Lower Columbia	55	97.6	45	93.2	96
Apr. 13	Cottonwood and Deer Islands	45	107.0	55	107.0	100
May 10	Crandall's	41	106.0	59	101.0	95
June 3	Clackamas River	64	112.0	36	112.6	100+

The only collections from the lower Sacramento River which were large enough to give significant data and in which the specimens were sexed are those from Woods Break, June 5 and 6, 1911, and from Tisdale wier, June 24–26, 1911. The sexes were quite evenly balanced in both of these collections, 52 per cent males in the first and 48 per cent males in the second.

The situation in the McCloud River is somewhat complicated by the presence of precociously matured males. Table 55 gives the percentages of males, both mature and immature, and of females for each collection made in the McCloud River. The sexes are present in approximately equal numbers, although there is a slight preponderance of females. Five and eight-tenths per cent of the total number of specimens are mature males. This signifies that between 10 and 12 per cent of the males which do not migrate during their first spring mature precociously during the following summer and fall.

TABLE 55.—PERCENTAGES OF MALES AND FEMALES IN McCLOUD RIVER COLLECTIONS.

Date.	Females.	Males.		
		Total.	Immature.	Mature.
FRY.				
1909:				
July	39	61	37	24
September	53	47	39	8
1911:				
September	42	58	49	9
October	56	44	43	1
November	57	43	39	4
December	50	50	49	1
YEARLINGS.				
1912:				
January	57	43	42	1
February	50	50	46	4
March	61	39	39	0
Average	51.6	48.4	42.6	5.8

RELATIVE SIZES OF MALES AND FEMALES.

Table 54 gives, for each Columbia River collection in which the specimens were sexed and which was large enough so that conclusions seem warranted, the average length of the females as a percentage of the average length of the males. Dividing this series roughly into quartiles, it is found that the average for the first six collections is 103.6; for the next five, 101; for the next five, 100.4; and for the last six, 98. The cumulative evidence seems conclusive that among the younger fish the females average slightly larger. In the case of the fish taken during and subsequent to September, however, this condition is reversed, and the males are slightly larger than the females. No explanation for this is offered, but the facts seem undoubted and worthy of record.

The males and females from the two collections from the lower Sacramento are approximately the same size. The length of the females in the collection from Woods Break averages 98.3 per cent of that of the males. In the collection from Tisdale wier the percentage is 102.4.

Table 56 gives for each collection made on the McCloud River the length of the females and of the mature males as percentages of the length of the immature males.

TABLE 56.—McCLOUD RIVER: LENGTH OF FEMALES AND OF MATURE MALES AS PERCENTAGES OF THE LENGTH OF IMMATURE MALES.

Date.	Males.		Females.
	Immature.	Mature.	
FRY.			
1909:			
July	100	145	107
September	100	112	98.3
1911:			
September	100	105	97.5
October	100	101.5	98.9
November	100	109	100
December	100	106	99.7
YEARLINGS.			
1912:			
January	100	136	98.2
February	100	115	101.2
March	100	....	98.6

There is apparently no significant difference in the length of immature males and females, but the mature males are distinctly larger than the immature specimens. This indicates either that they are slightly older or that they have, for some unknown reason, grown more rapidly than the other individuals of the same brood.

PRECOCIOUSLY MATURE MALES.

The precocious maturing of young chinooks has been noted by Rutter and is a phenomenon well known to many hatchery men. Most of these precocious males are, without question, the same age as the immature fish taken at the same time, but, as we have just shown, average distinctly larger (about 16 per cent). The time for maturing corresponds with the normal spawning time for the adult fish, late summer and autumn, although, as shall presently be shown, they may be found during the winter and spring, long after the normal spawning season is past. In addition to the precocious males from the McCloud River they have been also found in various collections from the Columbia River system, as follows:

1. Clackamas River, August 30 and 31, 1916: Four out of 10 specimens. Length of the mature males is 105 per cent that of the immature specimens.
2. Seufert, Oreg., September 2, 1915: Three out of 52 specimens. Length of mature males is 116 per cent that of immature specimens.
3. McKenzie River, September, 1916: Eight out of 11 specimens. Length of mature males is 122 per cent that of immature specimens. (These were collected from a pond used for holding spawning fish and have not previously been considered because of the small size of the collection and the great irregularities in size and scale growth.)
4. Hatchery ponds at Bonneville, Oreg.: Specimens of mature males were not infrequently found here during the spring of 1915, while the author was engaged in marking a series of yearling fish.

It will be noticed that the mature males are only recorded in collections from tributaries fairly well upstream.

In appearance these precocious fish are, when fully mature, strikingly different from the immature specimens. In addition to the greater size, the head is relatively larger, the body is deeper and thicker, the skin covering the entire body and fins is thickened so that the scales appear smaller, and the coloration is distinctly modified. The general color is a dark yellowish brown, becoming distinctly yellow ventrally. The color of the spots is deepened so that they are conspicuous even against the darkened background. There is also a tendency toward the development of bright yellow or rose-colored borders to the fins. The testes are large and white, in every respect resembling the testes of normal, mature, sea-run males. The scales are normal and show no absorption along the edges, as is so characteristic of the scales of spawning sea-run adults.

The habits of these fish do not apparently differ greatly from the habits of the immature fish with which they are associated. They feed regularly and are, to all appearances, fully as well conditioned as the others. This probably accounts for the fact that the scales are not absorbed at the margins. Rutter (1903) reports that they do not seem to be attracted by the females as are the sea-run adult males. Our observations are, however, to the contrary. The fish contained in the collection from the McKenzie River, made in September, 1916, were taken from a pond used for empounding spawning fish and the percentage of mature males is much higher than in any of the other collections. Rutter reports that the milt from such males will fertilize eggs normally.

The fate of these precociously matured males has been a matter of some speculation. It has been both claimed and denied that these died as do the sea-run adults after the spawning season. The writer had an opportunity in the spring of 1915 of testing this. He was at this time marking series of young blueback (sockeye) and chinook yearlings at the Bonneville (Oreg.) hatchery. Mature male chinooks, with fluid milt which could be expressed, were frequently encountered. A number of these were marked and held in a tank at the hatchery until July. Some had died in the meanwhile, but in some of those which remained the testes had practically recovered the normal immature appearance, and the characteristic coloration above described was much less conspicuous than it had been at the time the fish were marked and placed in the tank. The fish were apparently in perfect condition, and the scales show that they were growing actively at the time they were preserved. It is not known whether young males which have thus recovered from the effects of ripening the sex products will migrate to the sea.

PRACTICAL SUGGESTIONS.

Although information of still greater practical value may be expected to come from the study of the adult fish, some of the conclusions reached in this study appear to offer important suggestions, which may be applied in practical fish culture, as to the proper time for planting fry from the hatcheries.

In the early days of the artificial propagation of salmon it was an almost universal practice to "plant" the fry as soon as they were hatched. The mortality among the helpless alevins, encumbered by the heavy yolk sac, must have been enormous, and the hatcheries probably inflicted as much, or more, damage to the salmon runs as they did service of value. More recently the tendency among the more intelligent and scientific hatchery men has been to abandon the practice of planting alevins and to hold the fry at least until the yolk sac is absorbed. The system of holding and feeding fry after the yolk is absorbed has followed and with this, a not unnatural idea, that the longer the fish are held and fed the greater the chance of their surviving. The validity of this assumption is, however, dependent upon several factors which have not been sufficiently considered. The following more important ones may be mentioned here: (1) The possibility of an increasing percentage of loss among fish so held which would ultimately seriously reduce the number of fish planted; and (2) the effect of holding fish beyond the normal time of migration on (*a*) their chances for survival and return as adults, (*b*) the time of return as adults and whether they will return as spring or as fall fish,[a] and (*c*) the development of the normal feeding and protective reactions (instincts) which are essential to their survival after planting.

It is a well-known fact among hatchery men that salmon fry held and fed in hatchery ponds will, after a time, "go bad." At such times the fish usually refuse to eat well and show a distinct tendency to collect toward the lower end of the trough, tank, or pond in which they are held. If persistently held the loss rapidly increases but finally lessens as the critical period is passed, after which there is usually no more serious difficulty experienced in holding the fish. This critical period usually comes after the fish have been held and fed from 6 to 12 weeks—on the Columbia River in May or June and on the Sacramento River a month or two earlier, the exact time varying at different hatcheries and even in different ponds and tanks at the same hatchery. It has been shown above that the most normal time for migration on the Sacramento River is during the latter part of the spring, and on the Columbia River during the latter part of the summer. Therefore, it seems quite probable that these critical periods occur at times when the fry would normally quit the stream in which they were hatched and begin the seaward migration. There may or may not be a causal connection between these two phenomena, but even though the fry were allowed to leave the streams at these times—as the majority will, if permitted to do so—their time of migration would coincide well with the normal time observed, and the certain loss resulting from holding them over this critical period would be prevented. There is, of course, the possibility that this loss will occur under any circumstances, but such a conclusion is unwarranted from any data at present available.

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[a] The greater value of fish composing the spring run has been noted above (p. 5).

Suggestions, then, as to the care of fry are as follows:

1. The practice of planting alevins before the complete absorption of the yolk can not be too strongly condemned. No hatchery should be allowed to take a larger number of eggs than can be hatched and reared until the fry are at least ready to feed. Rather than plant the alevins before the yolk has been absorbed it would be infinitely better to allow the eggs which can not be properly accommodated in hatcheries to be deposited normally by the parent fish, and to thus rely upon natural propagation for the outcome.

2. The liberation of chinook fry at such a time as will enable them to migrate seaward at the normal migrating season for the stream in question is advised. This, on the Columbia and Sacramento Rivers, will ordinarily come within about three months after the fry have absorbed the yolk sac and begun feeding. Within this limit it would seem that the longer the fish are held and continue to feed well and grow normally (a point which should be carefully watched) the greater would be their chance for survival. If after several weeks' feeding the symptoms indicative of the approach of the critical period mentioned above appear, it would seem advisable to allow the fish to migrate. Where practicable the fry should not be liberated all at once, but should be allowed to begin the migration gradually and naturally, each fish leaving the parent tributary as the "instinct" to migrate develops. These conditions will be fulfilled if, at the proper time, the screens be removed from the retaining tanks or ponds so as to leave the way clear for the fry to enter the open stream.

These suggestions are of a general nature only. It is possible that in particular tributaries or in particular regions of a large watershed the conditions and habits of the fish are so different that these suggestions will not apply. In the absence, however, of definite information on these points the practical application of the above suggestions will, as a rule, be found advantageous.

SUMMARY.

1. Chinook fry first appear in the Columbia River as early as December of the same year in which the eggs are deposited. By March and April they are fairly numerous in the lower part of the river. Fry appear about two months earlier in the Sacramento River.

2. The average length of the youngest fry is between 35 and 40 mm. The rate of growth is especially rapid during the first five or six months, by which time the average stature for the first year has been attained. The average length of yearlings is approximately 100 mm. (4 inches), both in the Columbia and Sacramento Rivers.

3. The length of the scales and also the number of rings formed on the scales parallel quite closely the increasing length of the fish. Many of the youngest and smallest fry have not developed scales before migrating seaward.

4. Migration into the brackish water of the estuary is usually accompanied by an increase in the rate of growth, which is recorded on the scales as a marginal band of wide rings—the intermediate band. No intermediate band has been demonstrated on the migrating fry of the Sacramento River, but this is undoubtedly due to the lack of material collected at the right time and place.

5. The scales of fry remaining in fresh water develop a marginal band of narrow, winter rings during the latter part of the summer. The new growth of the second year begins soon thereafter.

6. The normal time for seaward migration among Columbia River chinooks is during the summer next succeeding the fall in which the eggs are laid. Seaward migrating chinook fry are, however, found throughout the year in the Columbia River, and the collections taken in March, April, and May include also migrating yearlings. There is, therefore, for each brood of fish, a period extending over about 18 months, during which the young may migrate seaward.

7. In the Sacramento River there is a distinct migration of fry lasting from January to June, inclusive. Although definite proof is lacking, it is probable that there is another period of seaward migration during the late autumn.

8. In the younger migrants of the Columbia, including practically all the fish migrating previous to June, the intermediate band is not to be distinguished from the preceding scale growth, due to the fact that the first few rings formed on the scales are always somewhat wider than the latter ones. After the first of June the intermediate band may be (but not always) distinguished as a marginal band of distinctly wider rings. Beginning in August or September this intermediate band may be preceded by a more or less distinct band of narrow rings that correspond to the winter band forming on the scales of upstream fish. The percentage of fish, whose scales show such a narrowing preceding the intermediate band, increases through the autumn and winter, so that by the following spring this narrowing becomes characteristic of the scales of all the yearling migrants. Although there is this average difference in the scales of fish migrating as fry during the fall and those migrating as yearlings in the spring, it is impossible, with our present knowledge, to distinguish in many individual cases between fish migrating at these two periods.

9. A sudden change in environmental conditions, such as removal from hatchery to wild conditions, may result in modified growth, recorded on the scales as a distinct break or check in the scale growth. This we have designated as the "primary check." Characteristically this appears as a more or less distinct narrowing of the rings succeeded by a series of wider rings.

10. There is apparently a distinct tendency for the larger specimens among the fish of any particular tributary to migrate earlier than the smaller specimens. It is

also apparent that the fish from the lower tributaries of a river system will, in a general way at least, migrate earlier than those from the higher tributaries.

11. Among the male fry which remain in fresh water over their first summer, about 10 per cent will mature precociously during the fall, the normal spawning period for adult sea-run chinooks. The proportion of male fry thus maturing presumably differs in different streams. These precociously mature males may recover from the effects of ripening the sex products, in this respect differing markedly from the known habits of the sea-run fish.

12. The suggestion is made that chinook fry be liberated from the hatcheries at such a time as will enable them to migrate at the normal period for seaward migration for the stream in question.

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EXPLANATION OF PLATES.

[The magnification of all photographs is the same, X 35. Abbreviations: *l* indicates lateral line; *c*, primary check; *g*, point distal to which is intermediate growth; *x*, check indicative of time of planting; *1st yr.*, first year of growth; and *2d yr.*, second year of growth.]

PLATE I.

FIG. 1.—Fry from Deer Island, Columbia River. April 13, 1916. Female, 51 mm. Part of skin from near center of body, showing scales with from one to five rings.

FIG. 2.—Isolated scale from the same specimen from which the skin shown in figure 1 was taken.

FIG. 3.—Fry from Point Ellice, Columbia River. June 12, 1916. Male, 68 mm.

FIG. 4.—Fry from Point Ellice, Columbia River. August 12, 1916. Female, 113 mm. Showing a weakly differentiated intermediate band not preceded by a band of narrow rings.

FIG. 5.—Fry from Crandall's seining ground, Grims Island, Columbia River. September 15, 1916. Male, 76 mm. Showing winter rings at the margin of the scale.

FIG. 6.—Fry from lake at Seufert, Oreg. September 2, 1915. Male, 83 mm. Showing check at *x* indicative of the time of planting.

FIG. 7.—Fry from Clackamas River. August 30, 1915. Female, 114 mm. Showing primary check and marginal winter rings.

FIG. 8.—Fry from McKenzie River. November 3, 1915. Male, 107 mm. Showing primary check and well-developed winter band at the margin.

FIG. 9.—Fry reared at Clackamas hatchery, Oreg. December 15, 1911. Male, 125 mm. A scale with but slight differentiation, characteristic of hatchery fish.

PLATE II.

FIG. 1.—Fry from Point Ellice, Columbia River. October 16, 1915. Female, 116 mm. Typical fall migrant, showing marginal winter band. No primary check.

FIG. 2.—Fry from same collection as figure 1. Male, 117 mm. Showing primary check and marginal winter band.

FIG. 3.—Fry from same collection as figure 1. Female, 110 mm. The intermediate band is preceded by a distinct band of narrow rings. No primary check.

FIG. 4.—Fry from same collection as figure 1. Female, 118 mm. Similar to figure 3, except that the primary check is present.

FIG. 5.—Fry from under cannery at Ilwaco, Wash. October 26, 1914. Sex not determined. 141 mm. The intermediate band is composed of unusually wide rings, characteristic of fish found under the canneries. The band of narrow rings preceding the intermediate band is conspicuous.

FIG. 6.—Fry from same collection as figure 5. Sex not determined. 166 mm. Similar to figure 5, except that the intermediate band is not preceded by a distinct band of narrow rings.

FIG. 7.—Fry from same collection as figure 5. Female, 145 mm. The check preceding the intermediate band (which is not strongly differentiated) is intermediate between the conditions illustrated in figures 5 and 6.

PLATE III.

FIG. 1.—Yearling from Deer Island, Columbia River. April 13, 1916. Female, 103 mm. Showing marginal winter band and no primary check.

FIG. 2.—Yearling from Crandall's seining ground, Grims Island, Columbia River. March 31, 1916. Male, 92 mm. Similar to figure 1, except for the primary check.

FIG. 3.—Yearling from same collection as figure 1. Female, 99 mm. A typical scale characteristic of the spring yearling migrants, showing an intermediate band preceded by a distinct winter band of narrow rings. No primary check present.

FIG. 4.—Yearling from same collection as figure 1. Male, 113 mm. Showing intermediate band and also primary check.

FIG. 5.—Yearling from Clackamas River. June 3, 1916. Male, 105 mm. Showing well developed new growth of the second year.

FIG. 6.—Sacramento River fry from Walnut Grove, Calif. April 9, 1911. Male, 75 mm.

FIG. 7.—Sacramento River fry from Butte Slough. June 8, 1911. Male, 97 mm.

FIG. 8.—Sacramento River fry from near Butte Slough. May 9, 1911. Male, 103 mm. Showing intermediate growth.

FIG. 9.—Fry from McCloud River. July 24, 1909. Mature male, 128 mm. Showing marginal winter rings.

PLATE IV.

FIG. 1.—Yearling from McCloud River. January 22, 1912. Male, 142 mm. Showing marginal winter band.

FIG. 2.—Yearling from same collection as figure 1. Male, 110 mm. Showing two wide marginal rings of the new growth of the second year.

FIG. 3.—Yearling from Brookdale hatchery, Calif. January 4, 1913. Female, 127 mm. Showing irregularities of growth characteristic of the scales of hatchery fish.

FIG. 4.—Yearling from Bonneville hatchery, Oreg. March 2, 1915. Male, 162 mm. The winter band is not strongly defined, but the new growth is well started.

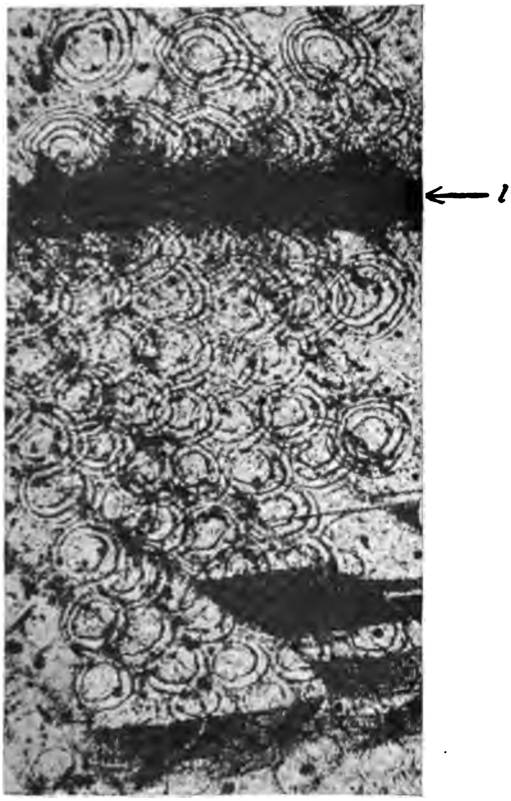
FIG. 5.—Yearling from Bonneville hatchery, Oreg. July 7, 1916. Male, 150 mm. This fish was one of the mature males marked in March or April and held until July. The new growth of the second year has begun, but is somewhat irregular.

FIG. 6.—Fry from Hope Island, Puget Sound. May 28, 1915. Male, 94 mm.

FIG. 7.—Yearling from same collection as figure 6. Male, 97 mm.

FIG. 8.—Young chinook taken in Half Moon Bay, Calif.

BIOLOGICAL STATION
BUREAU OF FISHERIES



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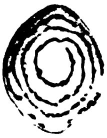

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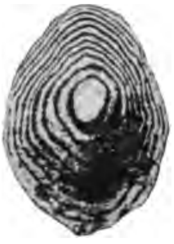

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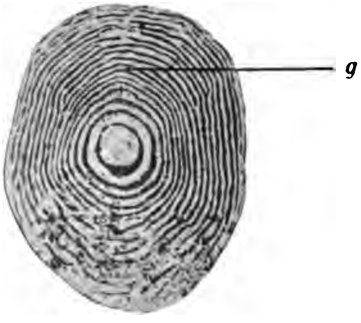

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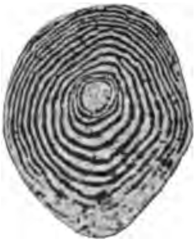

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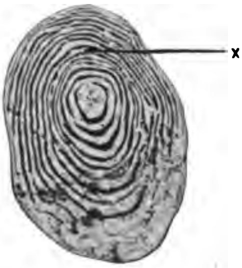

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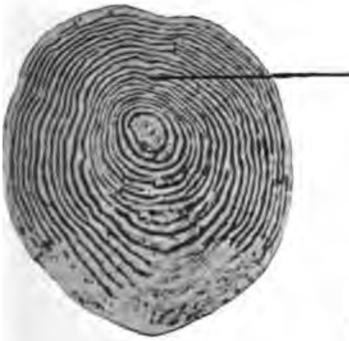

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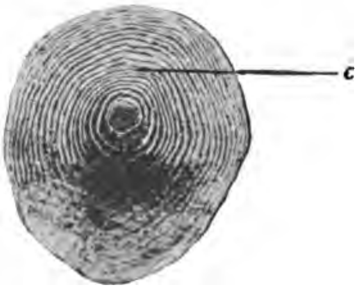

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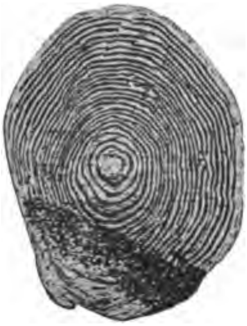

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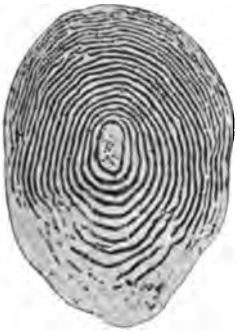

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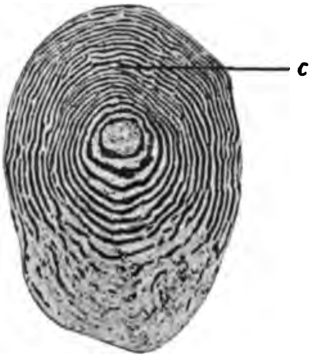

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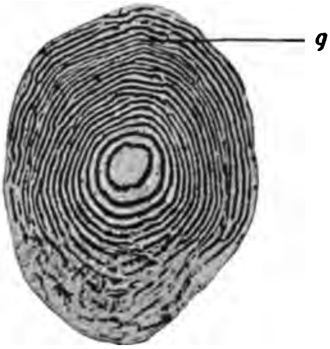

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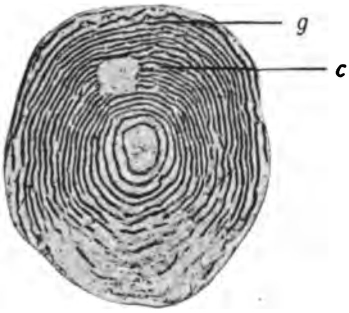

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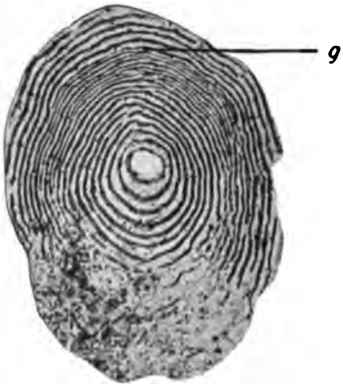

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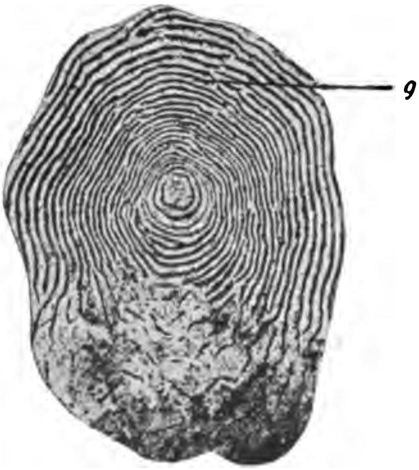

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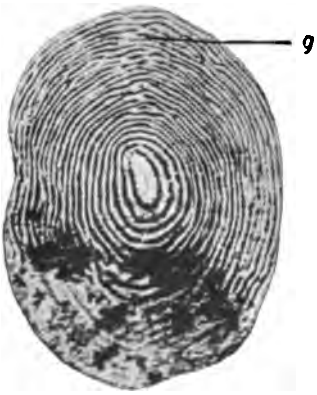

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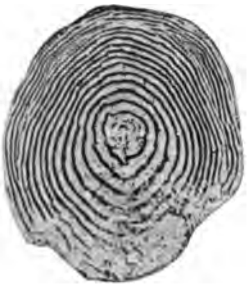

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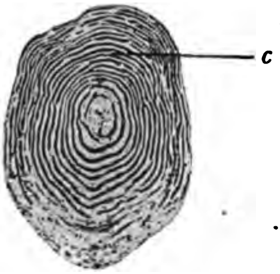

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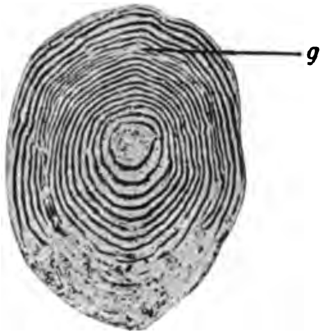

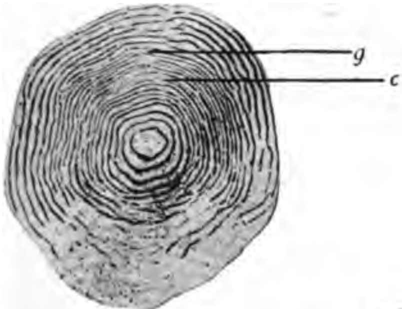

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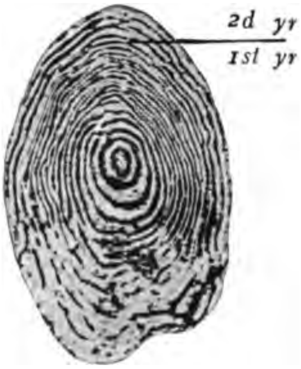

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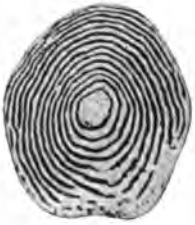

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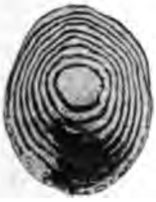

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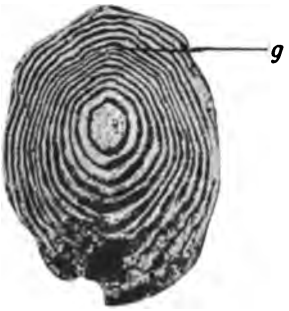

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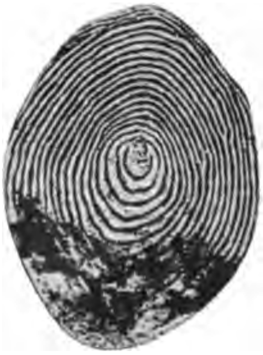

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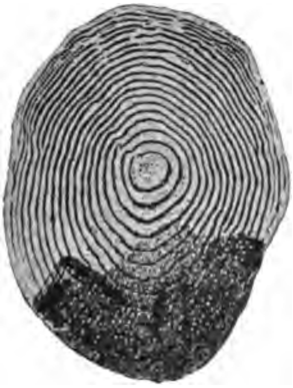

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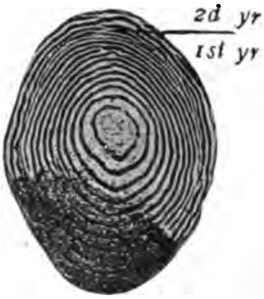

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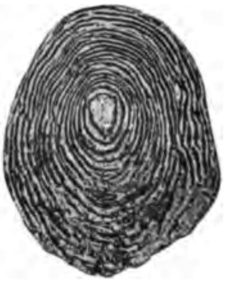

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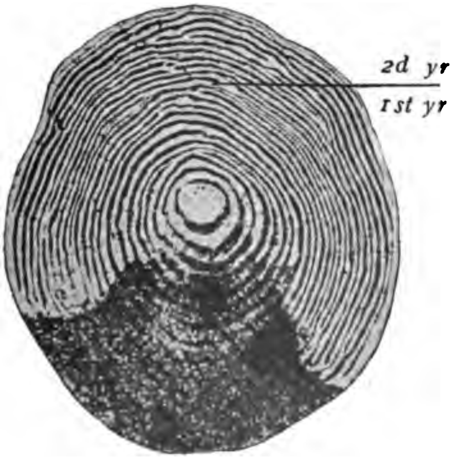

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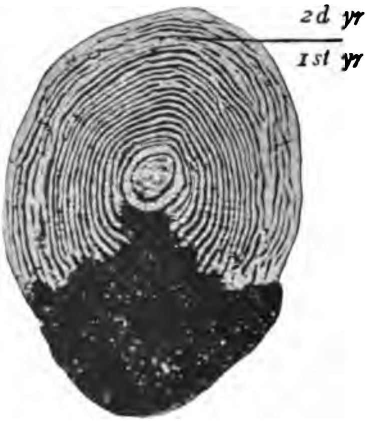

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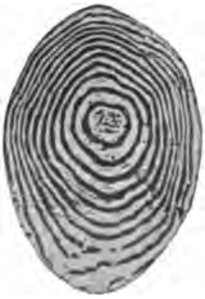

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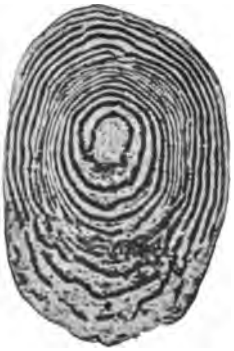

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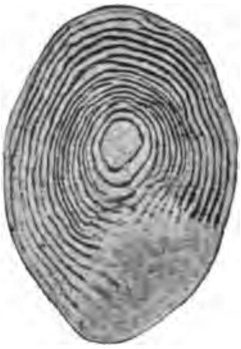

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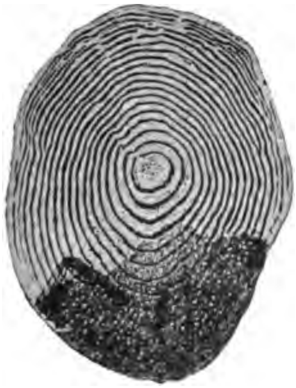
CONTENTS.

Page.

- Introduction 79
- Part 1. Natural history of fresh-water mussels 81
  - Habits 81
    - Conditions of existence 81
    - Locomotion 82
    - Density of population 84
    - Breeding 85
    - Winter habits 85
    - Feeding habits 86
  - Food of mussels 87
    - Significance of the problem 87
    - Observations of Franz Schrader on food of mussels 88
      - Species studied 88
      - Food content of waters 88
      - Food discrimination under normal conditions 89
      - Utilization of food materials 89
      - Experiments in feeding vegetable matter 89
      - Experiments in feeding animal matter 90
      - General observations 90
    - Observations of H. Walton Clark on food of mussels 91
    - Observations of A. F. Shira on food of juvenile mussels 93
  - Habitat 94
    - Body of water 94
      - Streams 94
      - Lakes 97
      - Ponds, sloughs, marshes, and swamps 100
      - Artificial ponds and canals 100
    - Bottom 101
    - Depth 107
    - Light 110
    - Current 111
    - Water content 113
      - Suspended matter 114
      - Minerals in solution 114
      - Dissolved gases 117
    - Vegetation 118
    - Animal associates 119
  - Parasites and enemies 121
    - Parasites 121
    - Enemies 122
  - Conditions unfavorable for mussels 123
    - Natural conditions 123
    - Artificial conditions 124
  - Growth and formation of shell 125
    - Measurements of growth 125
    - Presence of so-called growth rings 129
    - Mode of formation of shell 129
    - Significance of rings 132
    - Abnormalities in growth of shell 133



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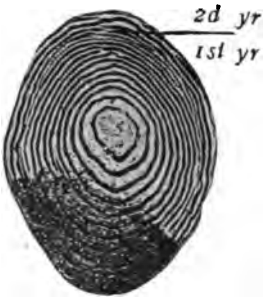

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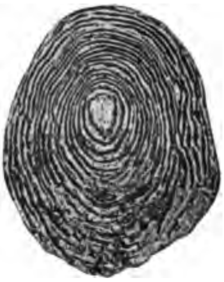

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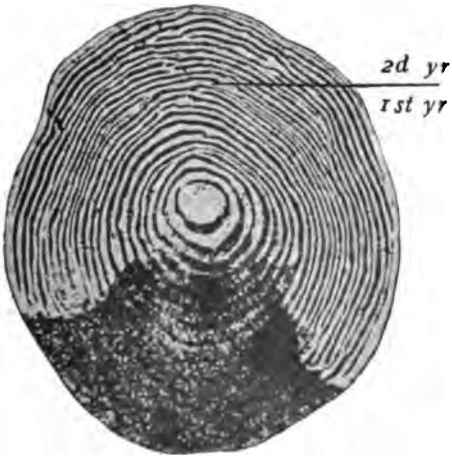

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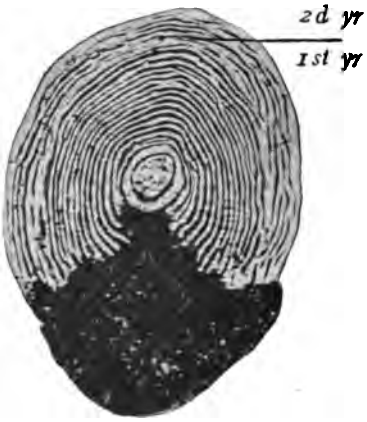

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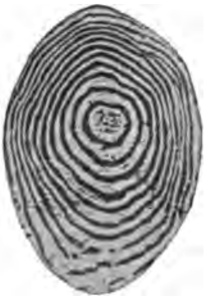

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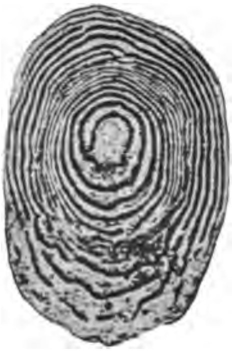

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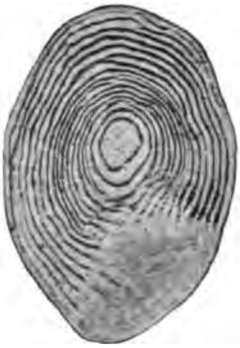

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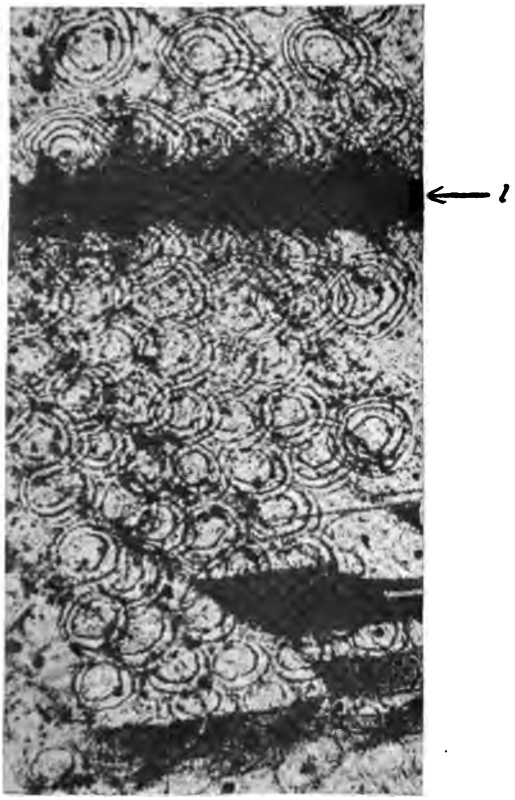

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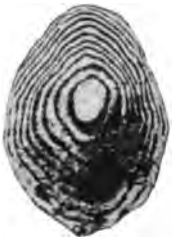

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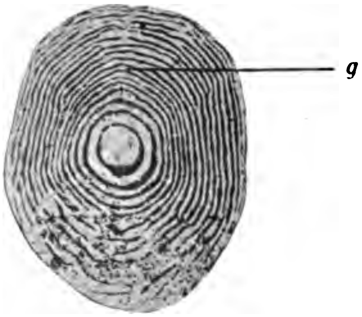

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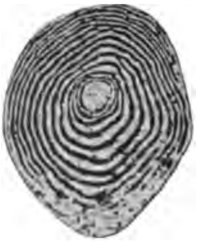

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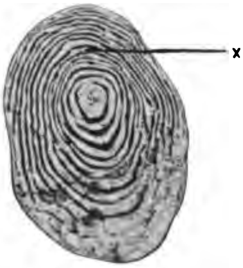

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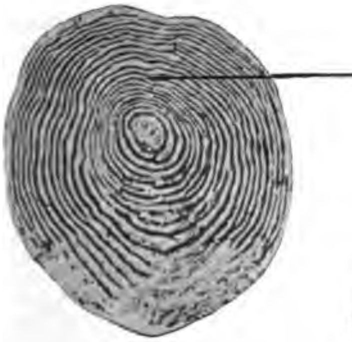

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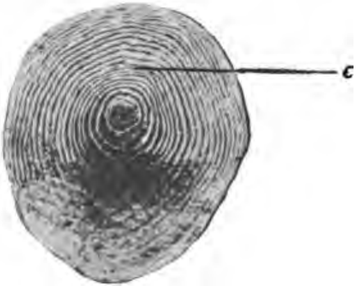

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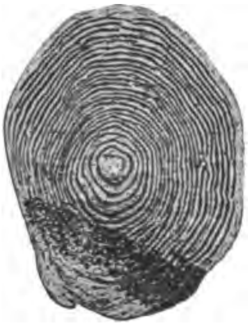

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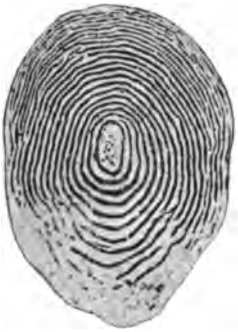

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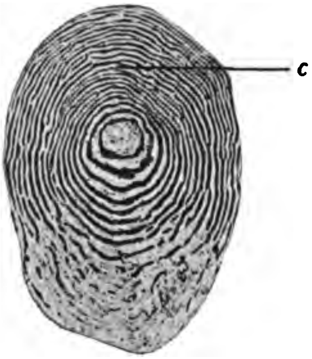

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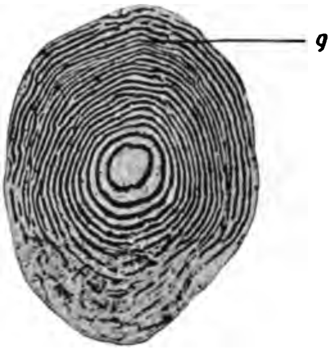

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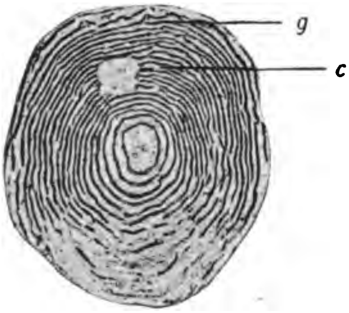

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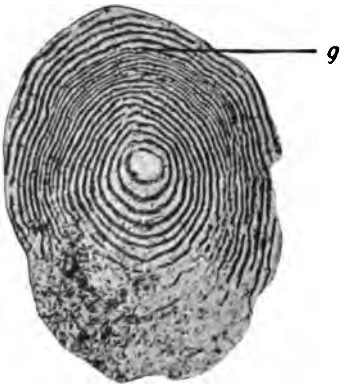

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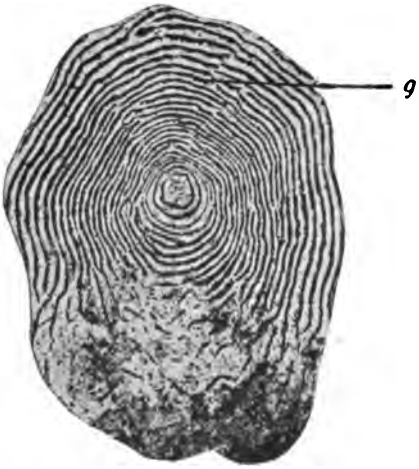

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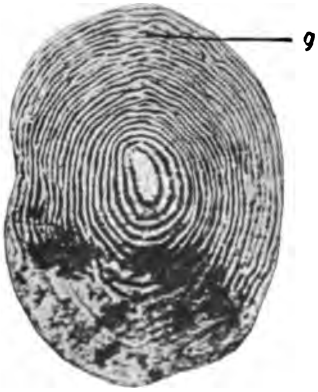

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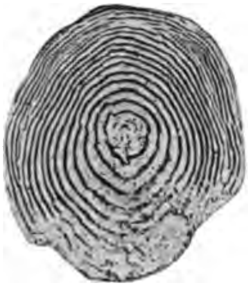

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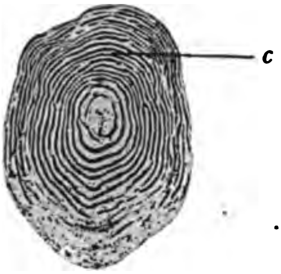

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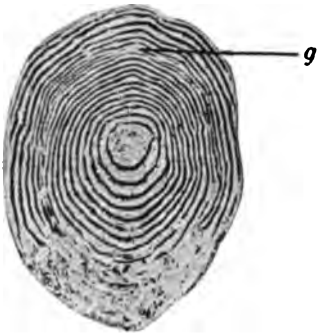

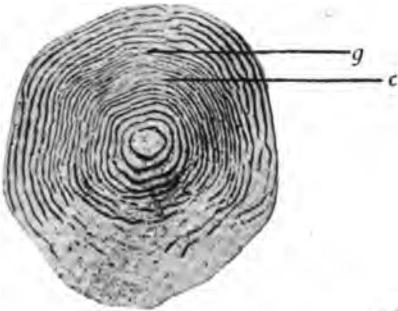

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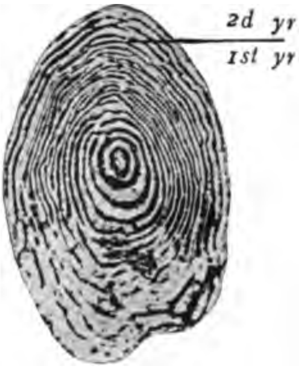

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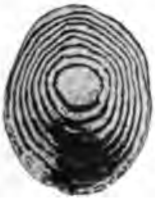

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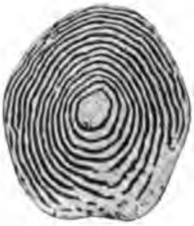

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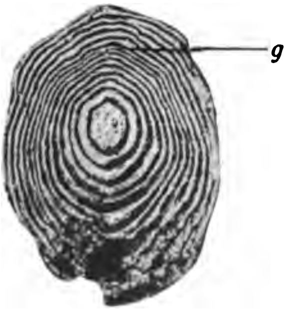

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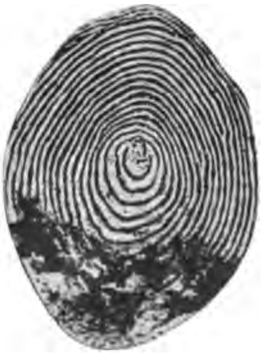

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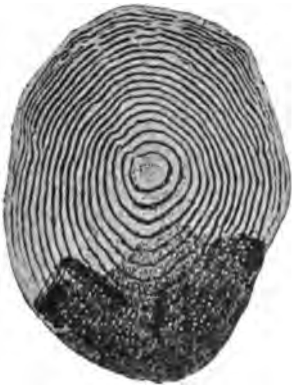

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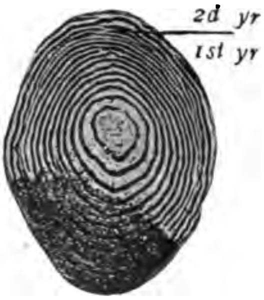

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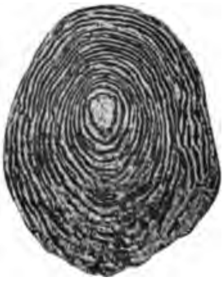

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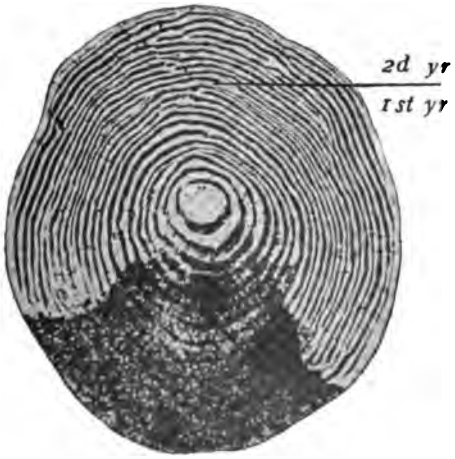

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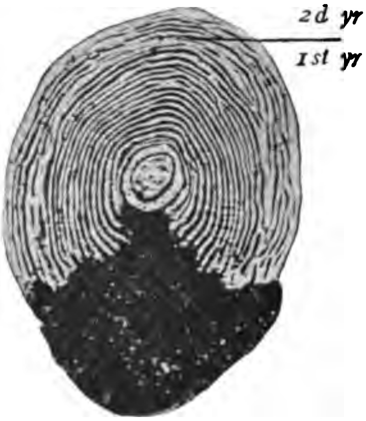

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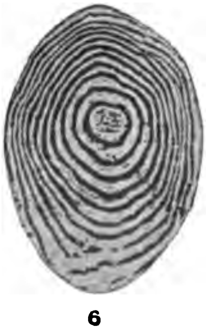

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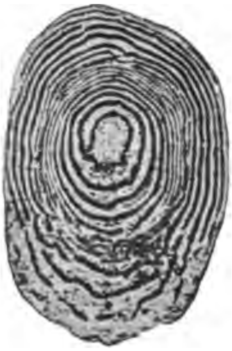

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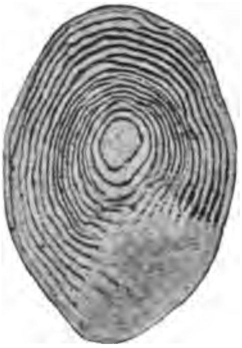

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consisted chiefly of the yellow mud of the river bottom, with organisms of any sort few and far between. In general, mud[a] is an abundant element in the stomachs of all mussels; so much so that the color and general appearance of the mass of the stomach contents of all river mussels examined was that of the bottom soil. In ponds full of diffused plankton algæ the plants may be present in sufficient quantities to at least fleck the "ground color" with a pronounced green or blue green. Studies of the stomach contents of the mussels in the reservoir of the Feeder Canal at Fort Wayne, in 1908, revealed the presence of many flagellates, such as Trachelomonas and Phacus, together with such minute plants as Scenedesmus, Pediastrum, Botryococcus, such diatoms as Gomphonema, Navicula, and the like, a few desmids (Cosmarium), fragments of *Ceratium hirundinella*, casts of the rotifer *Anuræa cochlearis*, and small fragments of confervoid algæ. In the main current of the St. Joseph, St. Mary, and Maumee Rivers there was much mud with about the same organisms scattered sparsely through it. A mucket, *Lampsilis ligamentina*, taken in the Auglaize River, contained what appeared to be bacteria. Mussels in Lake Amelia, near St. Paul, Minn., contained an abundance of that peculiar organism *Dinobryon sertularia*. The mussels of Lost Lake and Lake Maxinkuckee, Ind., contained enough plankton organisms of all the minuter sorts to give the stomach contents a greenish cast or to mottle it considerably with greenish flecks. Not to enter into too great detail, they contained such organisms as *Microcystis æruginosa*, *Pediastrum boryanum*, and *P. duplex*, *Cœlastrum microporum*, *Botryococcus braunii*, Scenedesmus, *Melosira crenulata*, *Coconema cymbiforme*, Navicula, *Epithemia argus*, Fragilaria, *Cocconeis pediculus*, and *Lyngbya æstuarii*. Melosira and Spirulina represented the longest filaments taken. *Anuræa cochlearis* was common but represented only by lorica, and Chydorus was the largest and most active organism taken.

Observations believed to be of both interest and importance were made in the Mississippi in the late summer and autumn of 1919. The river had remained high and swift until about the beginning of September, when it fell rapidly. With its fall the great body of marginal water lost the velocity of its flow, and great areas behind wing dams, lagoons, and mouths of sloughs became extensive areas of calm. In these a rich and varied plankton, consisting chiefly of holophytic sorts (Euglena, Pandorina, rotifers, Platydorina, and a bottom benthos of diatoms), rapidly developed in considerable quantities. The stomachs of the mussels in the bottom of these areas of calm contained numerous organisms of the plankton and benthos such as *Anuræa cochlearis*, Pandorina, Mycrocystis, Scenedesmus, Phacus, and various diatoms; the stomach contents bore general resemblance to those of the mussels of the Feeder Canal reservoir.

Opportunity was taken to examine the stomach contents of some young mussels which were obtained at the same time. In a slough sand-shell, *Lampsilis fallaciosa*, 19.1 mm. long, all that could be recognized was one colony of Clathrocystis. Another, 18.9 mm. long, contained chiefly brown, gritty mud in which were several *Scenedesmus caudatus*, *Phacus pleuronectes*, 1 Coscinodiscus, a few very minute Melosiras, and some rough spherical cysts. A third example, 19.6 mm. long, contained much brown flocculent organic mud, a large colony of Microcystis, 1 *Scenedesmus caudatus*, the diatom *Cyclotella compta*, and many of the green rough cysts.

The stomachs of some very small *Lampsilis anodontoides* and *L. luteola*, reared in troughs at Fairport and apparently thriving, contained only a fine brown flocculent mud, with rarely an occasional diatom. A young *L. anodontoides* from Smiths Creek bar in the Mississippi contained fragments of diatom shells indicating that it had been feeding on them to an unusual extent. Although Pleurosigma covered the mud of that region, forming an almost unbroken brown scum, it is noteworthy that it was only rarely found in the stomachs of the young mussels, it being apparently too large to enter the mouth.

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[a] The mud is probably mixed with much decomposing organic matter.

As regards the entire subject of mussel food and feeding there are some general observations it may be pertinent to make at this point.

At one time it was thought that extremely dense beds of mussels in the bottom of lakes might act as reducers of an excessive accumulation of plankton. They might indeed take care of many sunken and decaying plankton organisms, but under favorable conditions plankton can develop more rapidly than anything can eat it.

The finding of what appears to be bacteria in the stomachs of mussels of the Auglaize River and the observation made in tanks at the Biological Station at Fairport—that turbid water in which there were mussels cleared up rapidly, the mussels collecting the silt and other materials in suspension—raise the question as to whether mussel beds are not or can not be of use in the purification and sanitation of rivers. If oysters grown in polluted waters may harbor typhoid bacilli and so communicate the disease to those who eat them, there seems to be no good reason why mussels, which are not eaten, may not serve to arrest and devour those as well as other pathogenic organisms.

Since mussels are very inactive animals, the rate of metabolism may be expected to be low and the food requirements correspondingly small. The problem of obtaining nourishment for mussels is then one of the least of our troubles. Doubtless younger, more active mussels require a richer diet, and the first problem of mussel propagation, that of finding a suitable host, is fundamentally one of finding suitable nutrition for a creature remarkable for its fastidiousness in this regard. It may be that a critical problem is the finding of suitable nourishment for the first month or so of free life, but beyond this the only problem, so far as food supply is concerned, appears to be the avoidance of actually poisonous or harmful substances.

OBSERVATIONS OF A. F. SHIRA ON FOOD OF JUVENILE MUSSELS.

The following table (1) embodies a record of the stomach contents of 60 juvenile mussels, distributed among 6 species, taken in Lake Pepin during 1914. The material was studied with the use of a rafter counting cell, but since only a very small quantity of food could be obtained from each mussel the calculation of percentages can be only approximate.

TABLE 1.—FOOD OF SIX SPECIES OF JUVENILE MUSSELS TAKEN IN LAKE PEPIN, SEPTEMBER, OCTOBER, AND NOVEMBER, 1914.

Juveniles examined.		Length of juveniles (millimeters).			Percentage of food.			
Species.	Number.	Minimum.	Maximum.	Average.	Organic remains (principally vegetable matter).	Inorganic remains (silt, etc.).	Unicellular green algæ.	Diatoms.
Lampsilis luteola	12	5.0	15.4	9.5	89	6	3	2
Lampsilis ventricosa	10	4.8	13.4	8.8	90	5	3	2
Lampsilis alata	8	8.2	21.5	13.7	96	1	2	1
Lampsilis gracilis	10	6.6	19.6	13.5	95	1	3	1
Quadrula plicata	8	6.4	11.0	7.4	96	Trace.	3	1
Anodonta imbecillis	12	6.2	19.5	12.7	91	4	3	2

HABITAT.

The pearly mussels, as inhabitants of fresh water, are found in diverse habitats, in lakes and in rivers, in shallow and in deeper waters, in cold and in warm waters, in mud, in sand, and among rocks. Yet they do not occur in all lakes and rivers, nor in all parts of the lakes and rivers in which they do live; and the several species of mussels, when living together, are not always found in the same relative abundance. It may, therefore, be supposed that fresh-water mussels, like other animals, are adapted rather definitely to particular conditions of environment; that some find congenial environment in still or sluggish water, while others thrive best in strong currents; that a mud bottom supports certain species, while a firmer soil is required by others.

Adult mussels in some cases thrive, or continue to live at least, in environments where the young would perish, for delicately balanced conditions are required by very young mussels of many species, and only where these conditions exist can a mussel bed originate or perpetuate itself. On the degree of stability of the conditions favorable to the growth of the young the permanency of the bed must depend, since, when replenishment fails, the bed can continue only as long as the life of the adult mussels it contains. As any mussel has rather limited powers of independent locomotion, the place where it lives (or prematurely dies) is probably, as a general rule, near where it falls when it drops from its fish host; yet the early juvenile can be carried by the current, and doubtless this means of transportation may sometimes aid the young mussel in finding a suitable habitat. An adult niggerhead mussel lived in apparently healthy condition in a balanced aquarium at the Fairport station for nearly nine months; yet in nature this species is found only in strong currents, the favored environment of its fish host, the river herring.

The relationship of fresh-water mussels to the environment may be treated with reference to body of water, bottom, depth, light, current, water content, vegetation, and animal associates.

BODY OF WATER.

The various geographic types of fresh water in which mussels occur are rivers, lakes, ponds, sloughs, swamps, marshes, and canals. In so far as distinctive conditions characterize these various types of waters, each may have its characteristic mussel fauna. It may be said in general, that wherever conditions suitable for a particular species of animal prevail, that species will be found, except as it may have been naturally excluded through features of geologic history or other factors governing the distribution of animals; in the case of fresh-water mussels, however, emphasis must be placed upon a qualification of this general statement. Though all conditions in a body of water may be otherwise suitable, mussels can not naturally occur where conditions do not permit the entry and survival of the species of fish which serve as hosts.

STREAMS.

Mussels have undoubtedly reached their greatest development, as to numbers, both of species and of individuals, in flowing water. From the commercial standpoint, also, the quality of shells from streams is almost invariably superior. In general, where other conditions are favorable to mussels, larger bodies of flowing water are more productive than the smaller. Brooks do not usually contain mussels. Morphologically, mussels adapted to life in strong currents are differentiated from those adapted to still water by

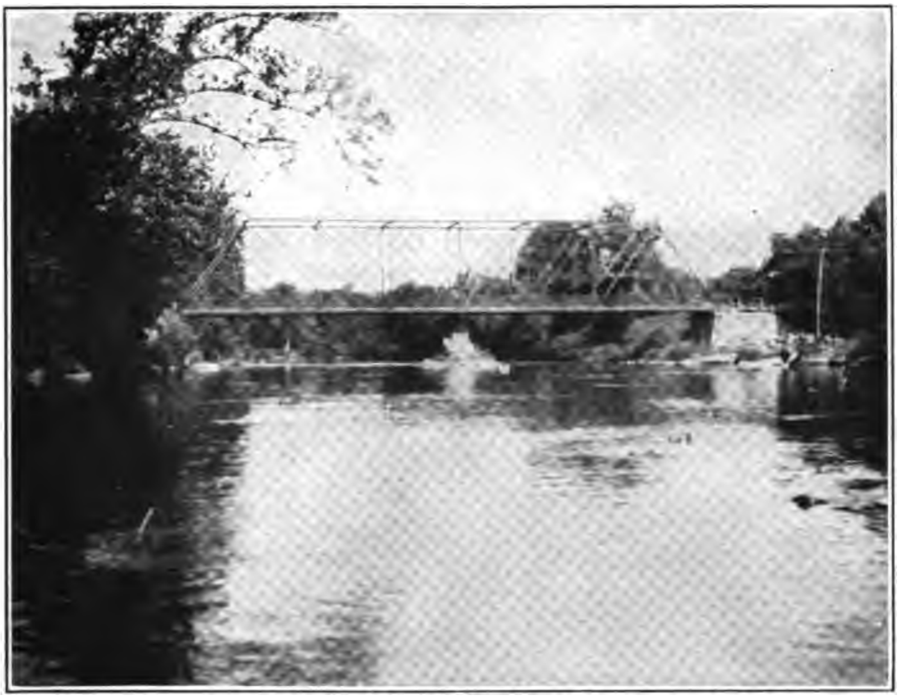

FIG. 1.—Upper waters of Grand River. Habitat of mussels in shallow swift water.

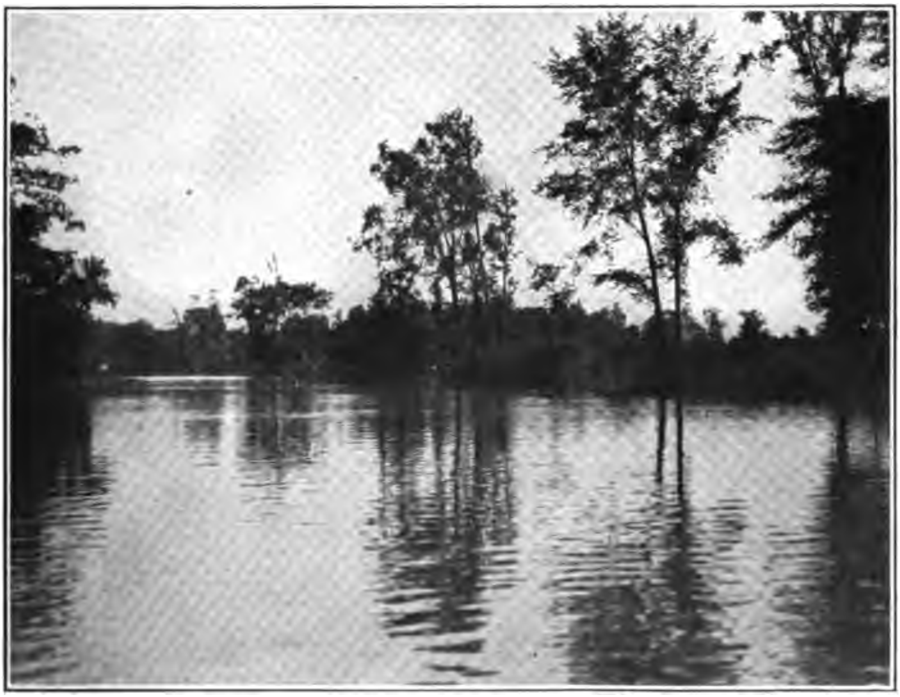

FIG. 2.—Upper waters of Grand River. Habitat of mussels in sluggish water.

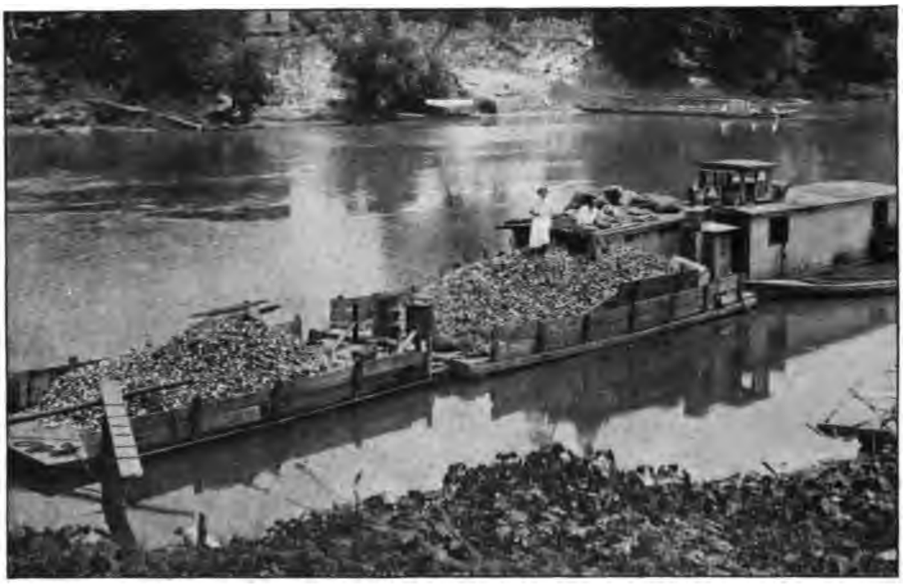

FIG. 1.—Black River, Ark., a very productive mussel stream.

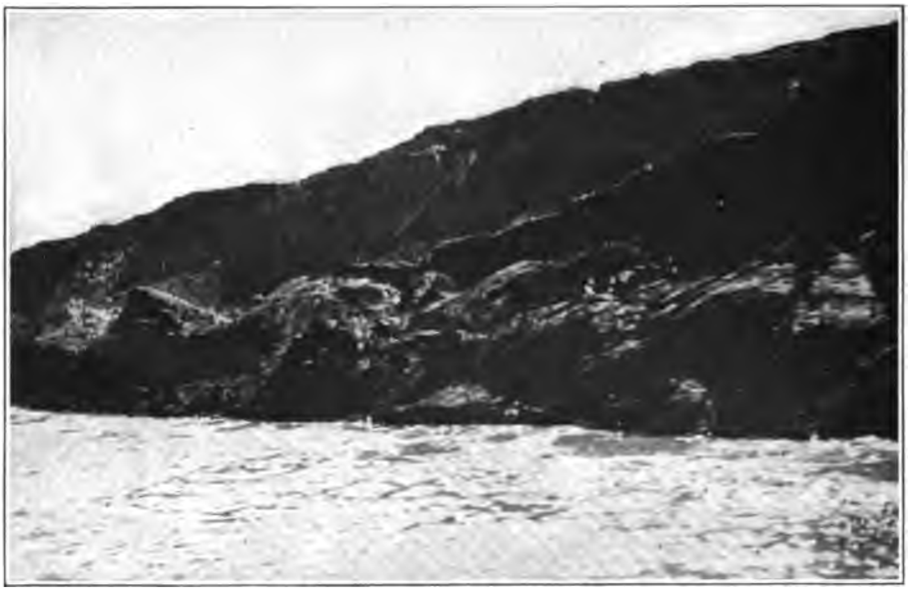

FIG. 2.—Red River, near Campti, La., a turbid stream with caving banks and shifting bottom, quite unfavorable for mussels.

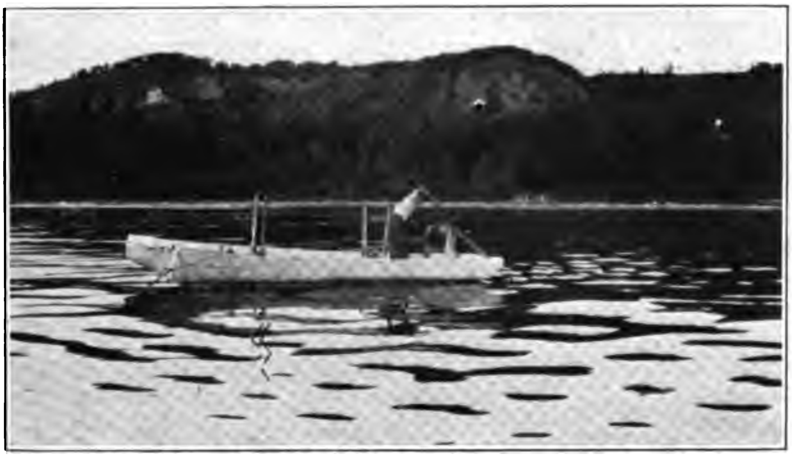

FIG. 1.—Lake Pepin, an expansion of the Mississippi River between Wisconsin and Minnesota, a favorable habitat for fresh-water mussels.

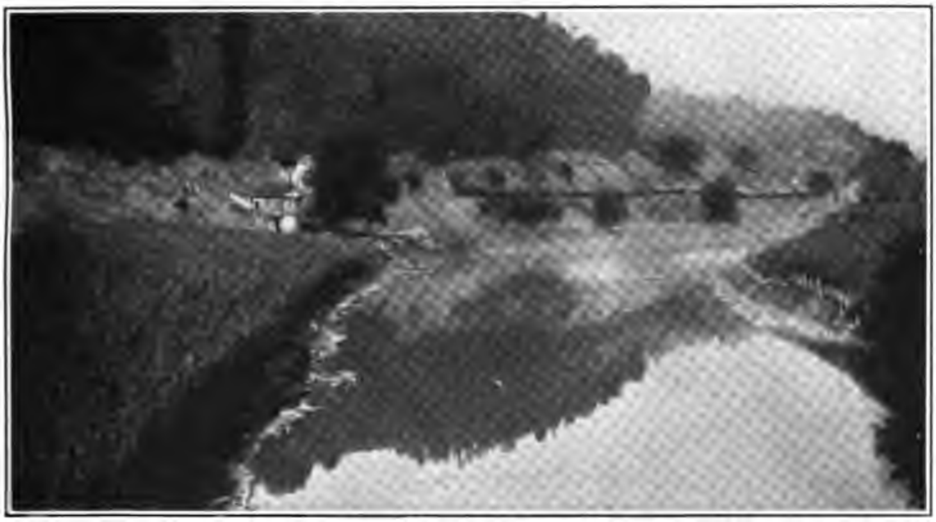

FIG. 2.—North Fork of Kentucky River, near Jackson, Ky., with sand bottom and conditions unfavorable for mussels. (Danglade.)

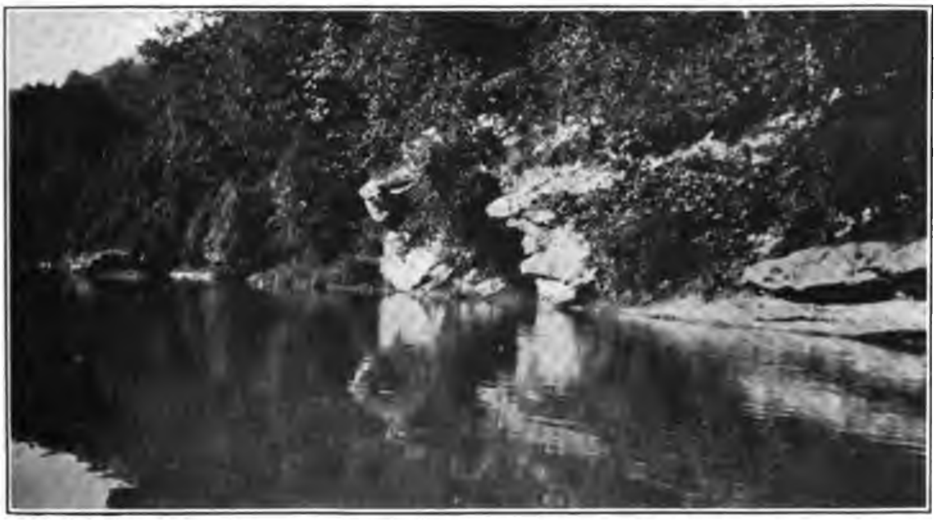

FIG. 3.—Tea Table shoals, another portion of the Kentucky River; the shores indicate stability, the water is moderately deep, and the environment is favorable for mussels.

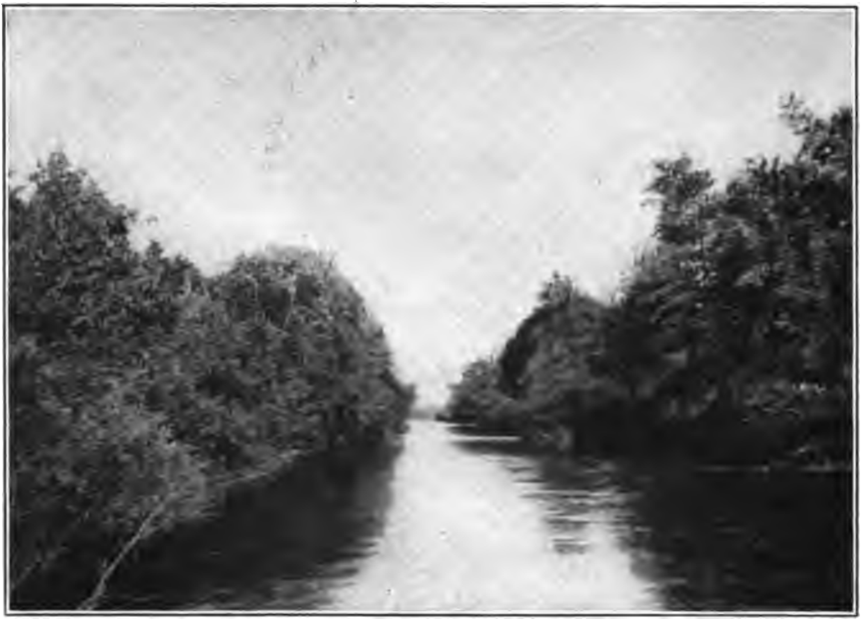

FIG. 1.—An undredged portion of the Kankakee River where valuable mussels flourish.

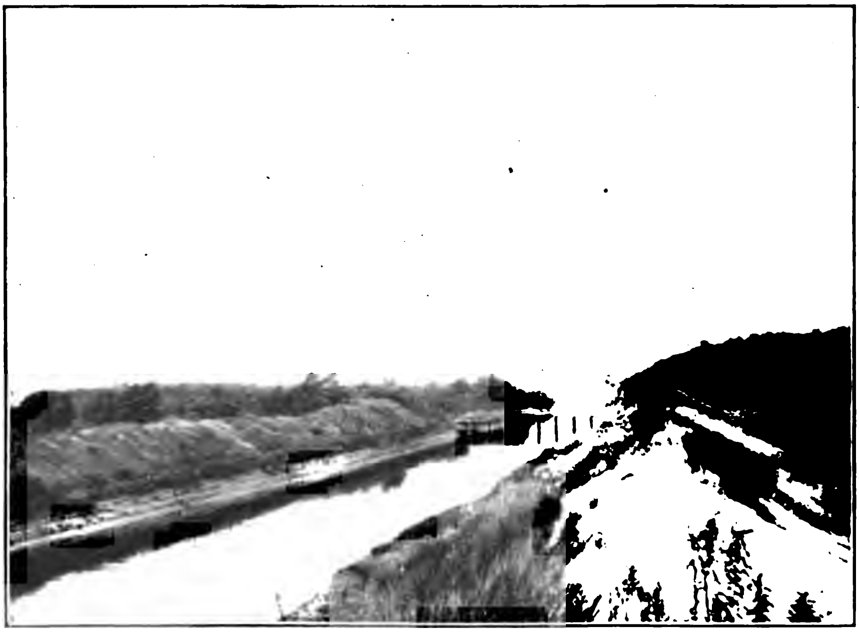

FIG. 2.—A dredged portion of the Kankakee River rendered (temporarily, at least) unfit for fresh-water mussels.

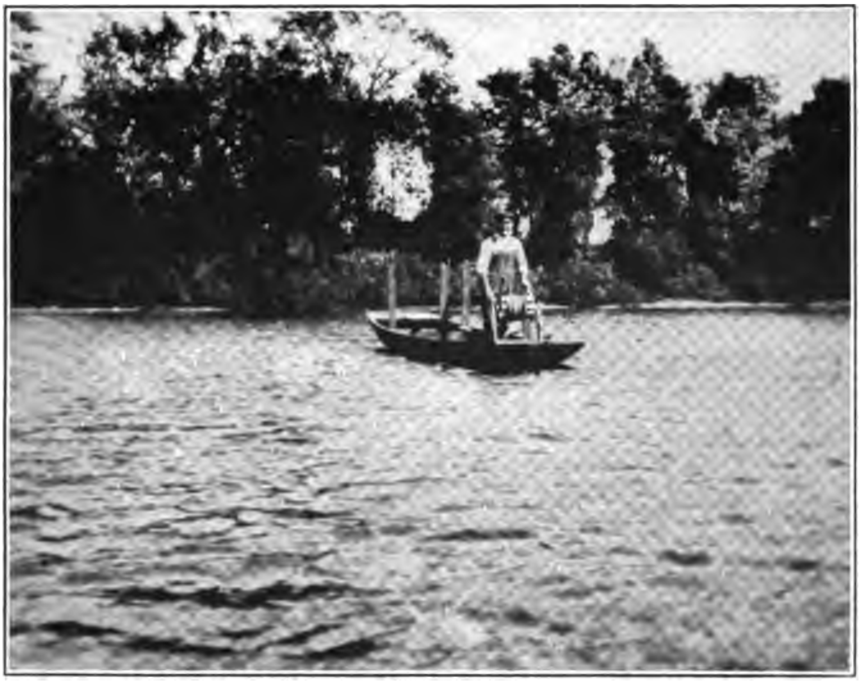

FIG. 1.—Lower portion of Grand River, Mich., where mussels thrive under natural conditions.

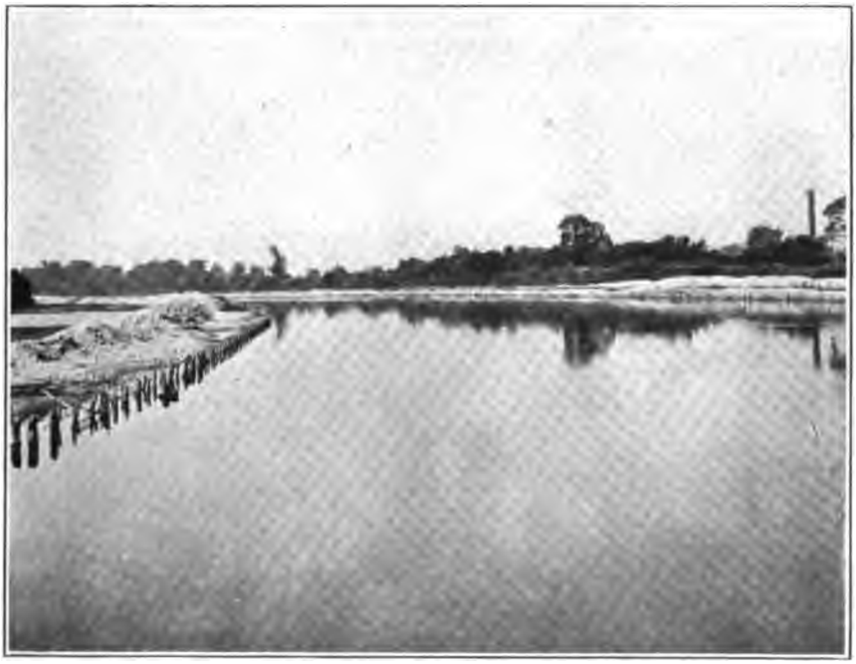

FIG. 2.—Lower portion of Grand River where conditions have been rendered unsuitable for mussels by canalization in interest of navigation.

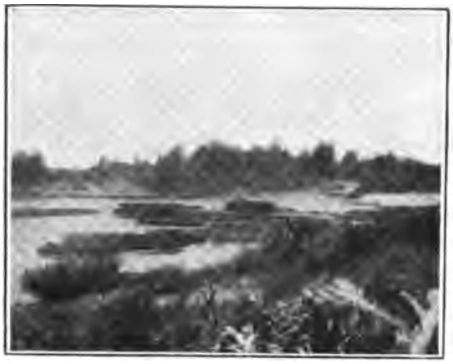

FIG. 1.—Auglaize River near Defiance, Ohio, showing islets and pools containing dense beds of mussels.

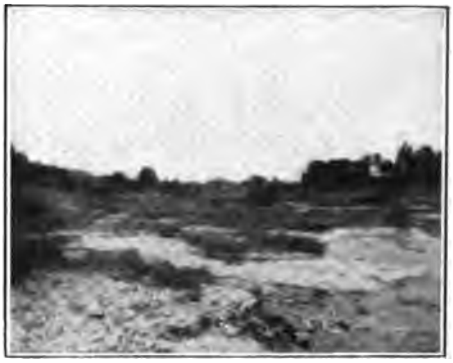

FIG. 2.—Maumee River, Defiance Ohio. The river bed a broad valley with limestone bottom, broken into numerous pools and channels with little islands —an excellent growth of fresh-water mussels.

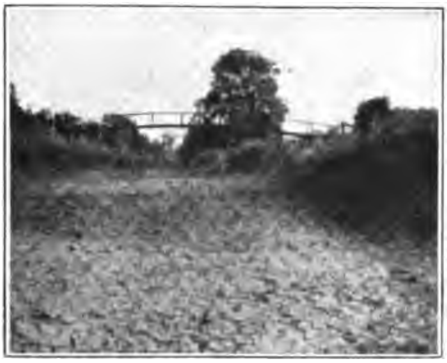

FIG. 3.—The draining of the Feeder Canal near Fort Wayne, Ind., revealed a remarkably dense population of fresh-water mussels.

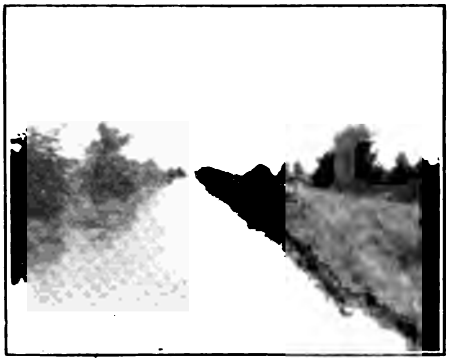

FIG. 4.—Parts of the Miami and Erie Canal afford excellent environments for mussels.

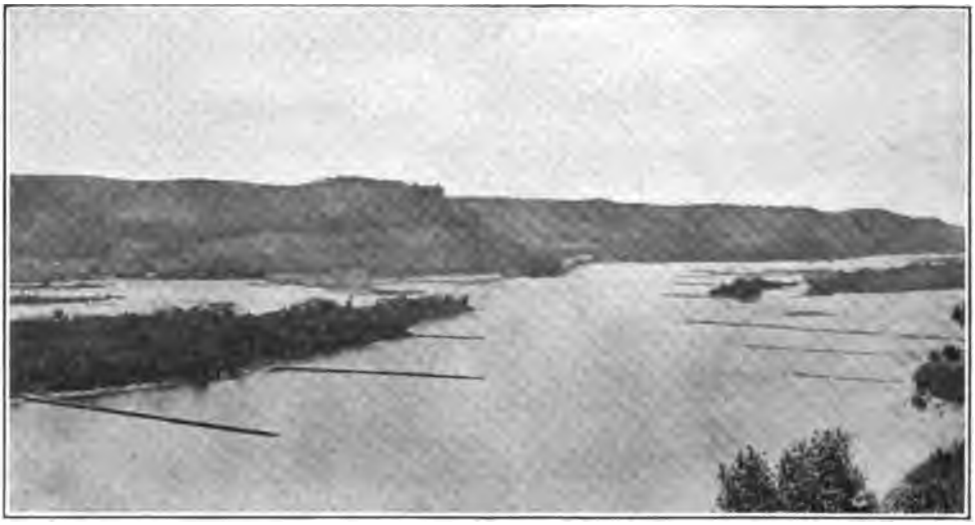

FIG. 5.—Construction of wing dams in the upper Mississippi River often renders conditions unfavorable for mussels that previously throve in such sections of the river.

the stronger development of the hinge teeth which aid in keeping the two valves of the shell in perfect apposition.

Since a river presents from source to mouth conditions of varying suitability for any form of animal life, there will usually be found in some measure a longitudinal succession of mussels. Shelford (1913, p. 122) gives a table showing the longitudinal sequence of eight species of mussels in the Calumet Deep River.

If one goes down a river from its headwaters, making collections of mussels at various points, many species may be found at each place, but some species first encountered may disappear before the upper waters are passed. Others appear here or there and perhaps disappear as one proceeds still farther down. The mussel fauna of the different sections of the stream are characteristic, although one or more species may be so adaptable as to live throughout the entire course of the stream.

This longitudinal succession of species is well illustrated by Table 2, which shows the distribution of mussels in the Grand River, Mich.

TABLE 2.—LONGITUDINAL DISTRIBUTION OF MUSSELS IN GRAND RIVER, MICH.[a]

Scientific name.	Common name.	Observations made at and below—							
		Outlets of headwater lakes.	Rives Junction.	Eaton Rapids.	Lansing.	Portland.	Ionia.	Lowell.	Grand Rapids.
1. Quadrula coccinea	"Flat niggerhead"	x	x	x	x	x	x	x	x
2. Strophitus edentulus	Squaw-foot	x	x	x	x	x	x	x	x
3. Anodonta grandis	Floater	x	x	x	x	x	x	x	x
4. Lampsilis ventricosa	Pocketbook	x	x	x		x	x	x	x
5. Quadrula rubiginosa	Flat niggerhead	x	x	x			x	x	x
6. Anodontoides ferussacianus	Small floater	x	x	x			x	x	x
7. Lampsilis iris	Rainbow-shell	x	x		x			x	x
8. Symphynota compressa		x	x	x		x			
9. Lampsilis luteola	Fat mucket	x	x	x					x
10. Alasmidonta calceola	Slipper-shell	x	x		x				
11. Unio gibbosus	Spike		x	x	x	x	x	x	x
12. Symphynota costata	Fluted shell		x	x	x	x	x	x	x
13. Lampsilis ellipsiformis			x	x	x	x	x	x	
14. Quadrula undulata	Three-ridge		x	x		x	x	x	x
15. Lampsilis ligamentina	Mucket			x	x	x	x	x	x
16. Alasmidonta marginata	Elk-toe			x	x			x	
17. Quadrula tuberculata	Flat purple pimple-back					x	x	x	x
18. Lampsilis recta	Black sand-shell					x	x		x
19. Lampsilis alata	Hatchet-back, pink heel-splitter							x	x
20. Quadrula pustulosa	White warty-back							x	x
21. Lampsilis gracilis	Paper-shell								x
22. Obliquaria reflexa	Three-horned warty-back								x
23. Obovaria ellipsis	Hickory-nut								x
24. Plagiola elegans	Deer-toe								x
25. Quadrula lachrymosa	Maple-leaf								x
26. Symphynota complanata	White heel-splitter								x
Total		10	14	14	10	12	13	16	22

[a] Observations by R. E. Coker in 1909.

SUMMARY OF TABLE.

Total species observed	26
Other species occurring above Portland	6
Species occurring throughout river	10
Species found only at or below Portland	10
Species not found below Grand Rapids	4
Species found only below Grand Rapids	6

It will be observed at once that a far greater number of species is found in the lower part of the stream. Thus, while only 10 of the 26 species observed in the river were found near the headwater lakes, 22 species were met in the section of the river between

Grand Rapids and the mouth at Grand Haven. It might be thought that this was due to the fact that there would be fewer obstacles to the passage of mussels downstream than to their distribution in an upstream direction. It seems sufficient, however, to assume that the unequal distribution is due rather to the greater variety of conditions of depth and of fish associates presented in the lower portion of the river. Shallow water only is found in the upper river, except as artificial pools have been formed in recent years by the construction of dams, while in the lower river deep water prevails in its channel and all lesser depths are found between the channel and the shores. The very breadth of the lower part of the river affords also a greater area for fish and mussels.

A difference of up-river and down-river habitat is presented by the distribution of two closely related species, the three-ridge, *Quadrula undulata*, and the blue-point, *Quadrula plicata;* the former, a more compressed and rougher form, is found in the more rapid waters of upstream habitats, while the latter, being thicker and less ridged, occurs in the deeper waters of the lower parts of a river system.[a] (See Clark and Wilson, 1912, and Wilson and Clark, 1912.)

In some rivers mussels are almost entirely lacking for long distances, as in the main course of the Missouri River for hundreds of miles above its mouth, where the absence of mussels is apparently due to the rapidly shifting bottom of sand. The Red River, with its heavy load of silt and its habit of suddenly cutting into its banks and changing its course, is manifestly unsuited for mussels, and examination of its bottom in many places by Isely (1914) and Howard revealed extremely few mussels (Pl. VII, fig. 2). There is also a virtual absence of mussels in the Mississippi River, except close alongshore, below the mouth of the Missouri River. Examination of the Musselshell River in Montana by J. B. Southall in 1919 revealed the presence in numbers of only a single species of mussel, and this a species (*Lampsilis luteola*) characteristic of lakes, which lived in the portions of the river deep enough to remain as isolated pools during the periods of dry weather. In the east fork of the Chicago River, Baker (1910) found only 3 species, and these were mussels characteristic of pond habitats, which were able to survive the dry seasons in the small ponds left isolated in the deeper parts of the river channel.

The James River, in North and South Dakota, though having very few fish, was found to possess a comparatively varied and abundant mussel fauna in the still waters between shallow riffles; but there was evidence that the mussels were derived from fish infected in other waters, that ascended the stream in times of flood (Coker and Southall, 1915).

The suitability of any section of a stream for the growth of mussels arises from a diversity of causes, including the nature of the rock or soil through which the stream is flowing, the character of the drainage waters entering the river at or above the section, the gradient of the stream bed with its effect upon depth and currents, and the species of fish which frequent the region.

Barriers in the course of a stream such as natural falls, or artificial dams, if impassable to fish, may have an effect upon the distribution of mussels. Wilson and Danglade (1914) found no mussels of the genus Quadrula above the Falls of St. Anthony in the Mississippi River, although several species of this genus are very common in the river below that barrier. Wilson and Clark (1914) found only 4 species of mussels in the Cumberland River above the Cumberland Falls (one of these probably planted), while 19 species were taken in the pool immediately below the falls, but in this case the conditions prevailing in the river above the falls appeared distinctly unfavorable for fresh-water mussels. An impassable dam formed after mussels were generally distributed throughout a stream would have little significance with reference to the distribution of mussels the hosts of which subsequently thrived both above and below the dam. The effect, however, of a dam in changing a region of rapids into a pool, might cause the mussel fauna of swift waters to give place to a fauna of slack-water habitat.

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[a] Ortmann (1920) has definitely shown, for certain species, that: "(1) The more obese (swollen) form is found farther down in the large rivers, and passes gradually, in the upstream direction, into a less obese (compressed) form in the headwaters; (2) with the decrease in obesity often an increase in size (length) is correlated; (3) a few shells which have, in the larger rivers, a peculiar sculpture of large tubercles, lose these tubercles in the headwaters." He ascertains also that these laws do not apply to all species.

Studies of rivers in cross section indicate that there may be quite definite distribution of life with reference to the banks. Shelford (1913) has discussed a horizontal arrangement of animals that is best illustrated in the cross sections of curves where there is a horizontal gradation in rate of current and in size of material in the bed of the stream. In the strong current only the coarsest materials are dropped, while the finest silt is deposited where the flow is most retarded. The depth of water is doubtless one factor governing the horizontal distribution of mussels, but the nature of the bottom material is of first importance. Howard (Survey of Andalusia Chute, Mississippi River, report in preparation) found in a branch of the Mississippi, following a comparatively straight course (not on rapids) and averaging 1,200 feet in width, that mussels were uniformly restricted to a border 200 feet from the shore line. (See table below.) Some mussels were found almost anywhere along this border, but occurring in beds at points where the channel touched the shore and where bottom conditions were favorable; depth seemed to be a minor factor as affecting the distribution.

The following table (3) indicates the results of a sample series of unit hauls taken at stated distances from the water's edge and so represents the distribution in a cross section of the river. It is not typical because of the narrowness of the bed on the left bank, but it illustrates in a general way the distribution found throughout the survey.

TABLE 3.—DISTRIBUTION OF MUSSELS IN ANDALUSIA CHUTE, MISSISSIPPI RIVER.

	From right bank.					Middle of river.	From left bank.				
Distance, in feet, from water's edge	35	85	100	200	300	400	300	200	110	60	20
Number of mussels per unit haul	13	3	0	0	0	0	0	0	0	12	32

Where there are rapids with bowlder or cobblestone bottom across a river of this size, it is known that mussels are not limited to such a border but are found at all points across the stream.

LAKES.

The mussels from some lakes are large and heavy-shelled, while in others they are small, thin-shelled, and stunted. These extremes represent the varied conditions which lakes present in respect to mussel life.

Lakes that have a free circulation of water seem to be favorable; such are those that are interposed in the course of a river. A favorable feature in such cases, no doubt, is the direct and free connection with streams that are well supplied with mussels. Examples are Lakes Pepin and Pokegama, Minn., and the former is noteworthy for the abundance of mussels produced. Though at first sight Lake Pepin might be considered no more than an expansion of the Mississippi River, further observation shows it to be a true lake in many of its characters, as in clearness of the water, depth, growth of vegetation, and virtual absence of current. In both of the lakes mentioned, a characteristic lacustrine species, the fat mucket, or Lake Pepin mucket, *Lampsilis luteola*, which is thin-shelled and worthless in ordinary inclosed lakes, attains so fine a commercial quality of shell as to appear almost as a distinct variety. Caddo Lake, La., which is interpolated in the course of a stream, possesses a rich mussel fauna and has been the scene of active pearl fishery (Shira, 1913). The small Rice Lake near La Crosse, Wis., which is, in effect, an expansion of a thoroughfare connecting the Black River, near its mouth, with the Mississippi River, also supports a varied and luxuriant mussel fauna. Where lakes are freely connected with rivers, as are those first mentioned, or as are others with short open outlets to the rivers, the lakes and rivers have many species of mussels in common.

In Lake Pepin, Shira (report in manuscript) found that the distribution of the mussels is confined wholly to the shore line and the flats within a maximum depth of 25 feet; no mussels at all were taken in the deep central part of the lake. In certain places the mussels were quite densely distributed, forming very well-defined beds, but as these beds were generally connected by areas of lesser population, a more or less continuous mussel bed was found to occur on each side of the lake. The largest and most extensive beds were located on a gravel bottom, or a mixture of gravel and sand. Several good though less extensive beds occurred on bottoms containing a considerable percentage of mud.

The upper end of the lake evidently serves as a settling basin for the silt poured in from the river proper, and for a distance of about 2 miles below the entrance of the river the lake is comparatively shallow with a soft oozy bottom. In this section of the lake very few mussels are found.

Shira records 32 species of mussels (report in manuscript). Ten of the most abundant species with the percentage of occurrence are given as follows:

	Per cent.
Fat mucket, *Lampsilis luteola*	31.5
Spike, *Unio gibbosus*	13.0
Blue-point, *Quadrula plicata*	12.7
Pig-toe, *Quadrula undata*	10.0
Pink heel-splitter, *Lampsilis alata*	8.3
Pocketbook, *Lampsilis ventricosa*	5.6
Slop-bucket, *Anodonta corpulenta*	5.5
Squaw-foot, *Strophitus edentulus*	4.3
White heel-splitter, *Symphynota complanata*	2.3
Black sand-shell, *Lampsilis recta*	1.4

In small lakes of considerable depth and without circulation, except as effected by winds and changes of temperature, animal life generally is absent or greatly restricted in the deeper portions, and mussels, when present, are confined to zones near the shores (Headlee and Simonton, 1904). Muttkowski (1918) in Lake Mendota found the optimum conditions for mussels at depths of 6 to 9 feet on sand bottom, but there was not an extensive mussel population in the lake as a whole.

The restriction of mussels to the border zones is indeed generally characteristic of the lakes of the Middle Western States, and even in this environment where the circulation effects of wave action may be felt, the mussels are stunted in growth. In their report on the mussel fauna of Lake Maxinkuckee, Evermann and Clark (1918, p. 251), summarize as follows the results of observations of mussels in lakes of Indiana and elsewhere:

> Generally speaking, lakes and ponds are not so well suited to the growth and development of mussels as rivers are; the species of lake or pond mussels are comparatively few and the individuals usually somewhat dwarfed. Of about 84 species of mussels reported for the State of Indiana, only about 24 are found in lakes, and not all of these in any one lake, several of them but rarely in any. Of the 24 species occasionally found in Indiana lakes, but 5 are reported only in lakes, and only 3 or 4 of the species common to both lakes and rivers seem to prefer lakes.

Characteristic species of mussels of inclosed lakes of upper Central States are named in the following table (4), and it may be remarked that the fat mucket and the floater are easily predominant over all others.

TABLE 4.—CHARACTERISTIC MUSSELS OF LAKES OF UPPER CENTRAL STATES.

Species.	Michigan.[a]	Minnesota.[b]	Indiana.[c]
Fat mucket, Lampsilis luteola	x	x	x
Floater, Anodonta grandis	x	x	x
Pocketbook, Lampsilis ventricosa	x	x	x
Squaw-foot, Strophitus edentulus	x	x	x
Small floater, Anodontoides ferussacianus		x	x
......, Quadrula rubiginosa	x		x
Spike, Unio gibbosus			x
......, Lampsilis subrostrata			x
Rainbow-shell, Lampsilis iris	x		x
Slop-bucket, Anodonta corpulenta		x	
Paper-shell, Anodonta imbecillis		x	
Paper-shell, Anodonta pepiniana		x	

[a] Coker, R. E. (unpublished notes).
[b] Wilson and Danglade (1914).
[c] Clark and Wilson (1912); Wilson and Clark (1912); and Evermann and Clark (1918).

While, as has been previously indicated, the plains streams, such as the Red River or the Missouri, with their ever-changing banks and bottoms and silt-laden currents, present conditions entirely unfavorable to mussels, yet the oxbow or cut-off lakes adjacent to them may offer favorable habitats for several species of mussels (Isely, 1914, and Howard, unpublished notes).

The sand shores of the Great Lakes to a depth of 8 feet are virtually barren of animal life (Shelford, 1918, p. 26). Fresh-water mussels are found in these lakes, chiefly, it appears, in the shallower bays, where they sometimes manifest a vigorous growth. They have not been used commercially to any extent, and probably few possess shells of a size and quality rendering them suitable for button manufacture.

In a biological examination of Lake Michigan in the Traverse Bay region, Ward (1896) encountered 9 species of mussels, all of species generally possessing relatively thin shells, while Reighard (1894) reported 20 species and subspecies from Lake St. Clair, of which the following 8 were described as abundant:

Pink heel-splitter, *Lampsilis alata* (Say).
Thin niggerhead, *Quadrula coccinea* (Conrad).
Spike, *Unio gibbosus* (Barnes).
Mucket, *Lampsilis ligamentina* (Lamarck).
...... *Lampsilis nasutus* (Say).
Black sand-shell, *Lampsilis recta* (Lamarck).
Pocketbook, *Lampsilis ventricosa* (Barnes).
Floater, *Anodonta grandis* (Say).

A more extensive list of mussels from Lake Erie and the Detroit River is given by Walker (1913), the list including 39 species of 15 genera. Since the great majority of the species named are those that normally possess thin and fragile shells, it may be supposed that the conditions in these waters are not favorable to the production of good shells. Certain species are mentioned, however, which, in other regions at least, possess shells of commercial quality. Principal among these are the following:

Maple-leaf, *Quadrula lachrymosa* (Lea).
Pimple-back, *Quadrula pustulosa* (Lea).
Pig-toe, *Quadrula undata* (Barnes).
Long solid, *Quadrula subrotunda* (Lea).
Hickory-nut, *Obovaria ellipsis* (Lea).
Black sand-shell, *Lampsilis recta sageri* (Conrad).

Clark, collecting on the shores of Lake Erie at Put in Bay, found dead shells all dwarfed in form but representing 14 species, of which the more common were as follows:

Three-ridge, *Quadrula undulata.*
Spike, *Unio gibbosus.*
Round hickory-nut, *Obovaria circulus.*
Paper-shell, *Lampsilis gracilis.*
Pink heel-splitter, *Lampsilis alata.*
Black sand-shell, *Lampsilis recta.*
Fat mucket, *Lampsilis luteola.*
Pocketbook, *Lampsilis ventricosa.*

PONDS, SLOUGHS, MARSHES, AND SWAMPS.

These types of environment are grouped together, since their mussel fauna is generally similar. The mussels are thin-shelled as a rule, since light weight is favorable for life in mud or soft bottoms and mass is not essential in the absence of current. Some possess narrow bodies and keel-like shells that fit them for locomotion through soft soil, and a few of the narrow-bodied species, where other conditions are suitable, have relatively heavy shells. Such are the pink heel-splitter, *Lampsilis alata*, and the white heel-splitter, *Symphynota complanata*.

The heavier mussels characteristic of rivers are sometimes found in sloughs, but in these the characters of flowing and still water are in a measure combined, since strong currents may prevail at seasons of high water. Sloughs, as parts of river systems and subject to being stocked from them, have mussel fauna to a certain extent related to that of the river; that is, the still-water species of the river are to be found in the sloughs. Marshes and swamps may have mussels at places where they contain pond or streamlike openings. In general the marsh and swamp environment is not favorable to mussels.

In ponds that are more or less isolated the thin-shelled mussels of the toothless type, as *Anodonta grandis* (floater) and *Anodontoides ferussacianus*, are characteristic. *Lampsilis parva*, one of the tiniest of fresh-water mussels, scarcely exceeding an inch in length, is sometimes found in such environments. A characteristic pond-dwelling species is the mussel *Unio tetralasmus*, which will survive in ponds that become dry in summer. Examples of this species of mussel have been found alive buried in the bottom three months after the water had disappeared on the surface (Isely, 1914, p. 18).

ARTIFICIAL PONDS AND CANALS.

Artificial ponds may present a favorable environment for many species of fresh-water mussels if the water supply is suitable, and some species are likely to become accidentally introduced with fish that are brought into the pond. The ponds of the Fisheries Biological Station at Fairport, Iowa, are supplied with water pumped from the Mississippi River. The first species of mussel to appear in the ponds was the large thin-shelled slop-bucket, *Anodonta corpulenta*, some examples of which had attained a length of 3 to 3½ inches when they were first discovered at the expiration of the second season of the pond, 17 months (May, 1910, to October, 1911) after the date of introducing water and fish into the newly excavated pond. Eighteen species which have been accidentally introduced are listed on page 165 below.

Few of these mussels are of commercial value, but it has been attempted to introduce several useful species by artificial infection upon fish, and success has been attained with the Lake Pepin mucket, a lacustrine mussel of high commercial value, which thrives well in the ponds and has attained a size and quality of shell suitable for commercial purposes at the age of 4½ years.

In canals mussels frequently thrive (Pl. XI, figs. 3 and 4). A mill race from a well-stocked stream seems to present a favorable environment for them. Clark and Wilson (1912, pp. 19–22) describe a luxuriant development of mussels in a canal at Fort Wayne, Ind., as follows:

> Toward the upper end of the canal, in a place where the bottom was 15 feet wide, the mussels were counted for a stretch of 10 feet along the canal bed and the following species noted: *Quadrula rubiginosa*, 11; *Q. cylindrica*, 1; *Q. undulata*, 86; *Anodonta grandis*, 6; *Ptychobranchus phaseolus*, 1; *Lampsilis ligamentina*, 5; *L. luteola*, 6. The width taken was the total width of the bottom of the canal and was considerably wider than the space occupied by the mussels.
>
> About a mile farther down the canal a space of 10 feet square was measured off in the bottom of the canal, and the following species were found: *Quadrula rubiginosa*, 6; *Q. undulata*, 60, all rather small; *Pleurobema clava*, 1; *Alasmidonta truncata*, 2; *Symphynota complanata*, 2; *S. costata*, 5; *Anodonta grandis*, 15; *Obovaria circulus*, 4; *Lampsilis ligamentina*, 5; *L. luteola*, 1; *L. ventricosa*, 4. This gave a little over one shell per square foot. In 1908, in a square meter of bottom near the Rod and Gun Club, the following species were noted: *Quadrula rubiginosa*, 9; *Q. undulata*, 36; *Symphynota complanata*, 1; *Anodonta grandis*, 17; *Obovaria circulus*, 11; *Lampsilis iris*, 2; *L. ligamentina*, 2; *L. luteola*, 3, giving a total of 81 per square meter. In addition to these shells there were many small Sphæriums, the ground being paved with them, 34 Campelomas, and 23 Pleuroceras. The square meter referred to above represents, as nearly as could be judged, an average number rather than either extreme.

It would appear from a general comparison of the aspect of mussels in lakes, ponds, and rivers that the effect of currents or circulation upon the growth of mussels is variable according to the relative proportions of organic and mineral foods present. In rivers, where the circulation of water is constant, mussels may grow to large size and possess thick shells, but when circulation is reduced, as in inclosed bodies of water, the mussels may be small and relatively thin-shelled, or they may attain a large size with thin shells (suggesting relative deficiency of mineral food), or else, with heavier shells, they may be dwarfed in size (suggesting a relative deficiency of organic food).

BOTTOM.

Most mussels are normally embedded in the bottom from one-half to three-quarters of their bulk.[a] That they may thus establish themselves, a firm but not impenetrable soil is required. The character of the bottom is, therefore, of especial significance to fresh-water mussels, though it has important relations to all bottom-dwelling animals. With regard to the bottom, consideration must be given both to its topography and to the materials of which it is composed. Major inequalities in topography, such as waterfalls and rapids, are discussed elsewhere. Minor inequalities are of importance because of the effects upon currents, sedimentation, light conditions, growth of food, and protective conditions; stability of soil is important for the establishment of the juveniles, for otherwise they will be overwhelmed. For some species objects for attachment, to which the byssus of the juvenile may be fastened, may also be necessary. Most of the varieties of bottom soil encountered are composed of one of the following materials, or of mixtures of two or more of them: Silt, mud, marl, clay, sand, gravel, pebbles, cobbles, bowlders, and ledge rock.

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[a] The cases of deep embedding mentioned by Wilson and Danglade (1913), where they give a depth of 1 foot or more for living mussels in Shell River (p. 15), and the report of a fisherman of 2 to 3 feet at Lake Bemidji, seem to be cases of "digging in" because of drought. *Unio tetralasmus* (Isely, 1914) and *Quadrula plicata* (Howard, 1914) seem to have a remarkable power of resistance under these conditions.

In rivers, sandy bottoms are regions of change comparable to sand-dune areas on land where immobile forms are killed. Sand bottoms occur extensively in many rivers and they may be veritable deserts. Rivers like the Missouri are devoid of mussels for hundreds of miles partly because of a preponderance of bottom of shifting sand. Mussels when found on sand bars in rivers are in transit seeking more stable conditions. Although comprising regions of instability in rivers where decided currents prevail, bottoms of sand may offer more favorable conditions in lakes where they furnish a permanent habitat for mussels.

A greater variety of bottoms favorable for mussels, as well as a more indiscriminate disposition of them, prevails in rivers than in the other bodies of water considered. In many lakes there is a more definite sorting of materials, leading especially to a segregation of the finest sediment in the deeper portions of the lake to form a bottom that is very soft and generally unsuitable for the Unionidæ; mussels possessing much mass would sink too deeply and have the gills too much clogged with silt to survive (Headlee and Simonton, 1904, p. 176). Where such conditions prevail the mussels are found near shore.

Headlee (1906, p. 315) summarizes observations and experiments in certain lakes of Indiana in the following words:

> The work of 1903 and 1904 shows conclusively that the mussels of Winona, Pike, and Center Lakes can not exist on the fine black mud bottom—they become choked with mud and apparently smother—and that the light-weight forms and the forms exposing great surface in proportion to weight can rest on top of comparatively soft mud and can, therefore, live farthest out on the deep-water edge of the bed. Because the mussels can not occupy any region where the pure black mud is present, they are confined by it to isolated beds and narrow bands of shore line.
>
> I believe that the whole evidence of the distributional and experimental work of 1903 and 1904 points clearly to the character of the bottom as the great basal influence in the distribution of mussels in small lakes generally.

The species he dealt with were the fat mucket, *Lampsilis luteola*, *Lampsilis subrostrata*, *Quadrula rubiginosa*, *Anodonta grandis*, and other small species with light shells. While his conclusion accords generally with the observations of the writers in other waters, the exclusion of mussels from mud bottoms can not be taken as an invariable rule. In the Grand River, at Grand Rapids, Mich., for example, one of the authors has observed such a heavy-shelled mussel as the three-ridge, *Quadrula undulata*, living in considerable numbers along with the light floater (Anodonta) in very soft mud. Also, in Mississippi Slough, in the Wisconsin lowlands along the Mississippi River opposite Homer, Minn., the blue-point, *Quadrula plicata*, the pimple-back, *Q. pustulosa*, and the pig-toe, *Q. undata*, have been found in considerable numbers on a soft-mud bottom along with the heel-splitters, *Symphynota complanata* and *Lampsilis alata*, and the slopbucket, *Anodonta corpulenta*, Baker (1918, p. 117) gives a summary of results of studies of mussels with reference to bottom and depth in Oneida Lake, N. Y., in the following words:

> The greatest number of individuals occurred on a clay or sandy-clay bottom. Twice as many mussels occurred in water deeper than 6 feet than within the 6-foot contour. These features are expressed in Table No. 27, the figures being averages per unit area of 9 square feet.
>
> TABLE NO. 27.—AVERAGE NUMBER OF MUSSELS ON BOTTOM.
>
> | | |
> |---|---|
> | Bowlder and gravel bottom | 6.14 |
> | Sand | 6.39 |
> | Clay and sandy clay | 13.00 |
> | Mud | 10.26 |
> | Within 6-foot contour | 7.84 |
> | Outside 6-foot contour | 16.85 |
>
> The above table shows that mussels are more abundant on the mud bottom in deep water (8 to 14 feet) than on sand, gravel, bowlder, or clay in shallow water (1 to 6 feet). These are the only studies of this character known to me.

In that lake one species, *Anodonta implicata*, is reported from one kind of bottom only, in sand between bowlders; while another species, *Lampsilis luteola* Lamarck, is said to be common on all varieties of bottom, except gravel (Baker, 1918, pp. 161, 162).

Muttkowski (1918) found that sand bottoms marked the favored environments of fresh-water mussels in Lake Mendota, Wis.

In Lake Pepin most of the adult mussels are found on a bottom of gravel or a mixture of gravel and sand. Bottoms composed largely of mud but made firm by a mixture of sand or gravel or both, yield a good supply of mussels; such areas are of much less extent in the lake than bottoms of gravel or gravel and sand. Of 1,397 juvenile mussels comprising 16 species collected in Lake Pepin in 1914, practically 95 per cent were taken on a sand bottom; about 4 per cent, principally *Anodonta imbecillis*, were found on a mud bottom; and the remaining 1 per cent on gravel or a mixture of sand, gravel, and mud (Shira, report in manuscript).

In ponds and sloughs there is less choice of bottoms than in lakes, and mud bottoms usually prevail; for such conditions *Lampsilis parva*, *Lampsilis subrostrata*, the light-shelled Anodontas, and similar species are especially adapted.

When we consider the relation between various mussel species and the bottom in rivers, we find the matter complicated by several considerations. This much, however, may be said definitely: No mussels can survive in a shifting bottom, nor upon a bottom of solid bare rock. Between the extremes, beginning with clean sand or soft miry silt and ending with coarse gravel and bowlders or stiff clay, there is a great variety of bottoms utilized to a greater or less extent as habitats for various species of mussels.

There are, of course, more or less definite relations between bottom and other features. Soft, muddy bottom is always associated with a current that is feeble at least near the bottom, or with the checking of the current; gravel bottom is usually associated with swift current; and clean sand or gravel is associated with clear water. Certain of the "mud-loving" mussels, such as the Anodontas, may be really lovers of quiet places and their association with mud rather an accident. Some of those supposed to be partial to sandy or gravelly bottom may simply prefer clear to turbid water. or may thrive best in a swift current.

Several species, including most of the Anodontas, *Symphynota complanata*, *Arcidens confragosus*, and others, are confined chiefly to one sort of bottom. A great many, however, seem indifferent to the character of the bottom, provided other conditions are favorable. Mussels may also apparently thrive where one would naturally think conditions unfavorable and where they might not survive if artificially planted. Thus in the crescent-shaped bayous along the Kankakee *Quadrula undulata*, and in sloughs of the Mississippi a closely related mussel, both heavy-shelled species, are found thriving on the top of deep, soft, silty mud which would not seem stiff enough to bear their weight.

In the Grand River, Mich., various species of mussels were found upon "clean" sand bottoms, but always sparsely. *Quadrula undulata* and *Lampsilis ellipsiformis* and *ventricosa* seemed best adapted to life in accumulations of drift. In sewage and waste-polluted waters at Lansing, Mich., *Lampsilis ligamentina*, *ventricosa*, and *ellipsiformis*, *Quadrula coccinea*, *Symphynota costata*, and *Alasmidonta marginata* were found in apparently healthy condition. The *Lampsilis ellipsiformis* obtained there, of especially large size, bore innumerable (but worthless) small pearls. (Coker, unpublished notes.)

In the Mississippi River near Fairport, Iowa, bottoms of unmixed mud and pure sand were found to be much less occupied by many of the species than mixtures of gravel and sand or of sand and mud, which supported both a far greater number of individuals and a somewhat greater variety of species. The preference for certain bottoms is most conspicuous when the proportion of the total catch of mussels found on the favored bottoms is viewed in connection with the proportions of these bottoms in the total area surveyed. Table 5 shows the total number of mussels taken from the different types of bottom in a survey of Andalusia Chute, Mississippi River (Howard, report in preparation):

TABLE 5.—MUSSELS COLLECTED IN SURVEY OF ANDALUSIA CHUTE, WITH REFERENCE TO CHARACTER OF BOTTOM.

Composition of bottom.	Approximate percentage of total area of bottom.	Number of mussels.	Number of species.
Mud	7	44	17
Mud and sand	4	158	20
Mud and ledge rock	⅛	17	7
Sand	71	87	23
Sand and gravel	9	289	28
Sand and pebbles	½	29	12
Gravel (pure)	2	5	3
Gravel, cobbles, and rock	2	34	14
Gravel and mud	1	....	....
Pebbles	1	....	....
Rock	2	....	....

The niggerhead mussel, *Quadrula ebenus*, in some streams, at least, is said to show a decided preference for firm bottoms, as of gravel or blue clay, but few observations have yet been made upon these mussels in streams having considerable areas of clay bottom. In the Grand River, Mich., the pink heel-splitter, *Lampsilis alata*, was found living in a ledge of very tough slippery blue clay (Coker, unpublished notes). So firm was the clay that a mussel could be extricated from it only by the exertion of considerable muscular effort. Several other species of mussel were in the vicinity, but none were embedded in the clay except one example of the three-ridge, *Quadrula undulata*, and that was in a spot where the clay was mixed with mud and was distinctly softer. Some spikes, *Unio gibbosus*, were found lying on the blue clay but not embedded; it seemed evident that they were unable to penetrate so tough a bottom.

The character of the soil has an effect upon the amount of materials carried in suspension in the water. If the amount is too great, as over soft mud or over extremely fine sand, under some conditions the mussel becomes smothered, or having no chance to feed, is starved. Too much decomposing organic matter in the soil is said to cause enough acidity to attack and erode the shell. For several reasons, therefore, areas of rapid silt deposition, or soft-mud bottoms, are quite unfavorable to mussels. Mussels are usually found in rivers in places where the bottom is swept clean by the current, even though in flood time the water may be heavily laden with silt in suspension.

The selection by some species of bottoms of gravel, pebbles, and bowlders as most favored habitats can readily be understood from the foregoing remarks; but there are still other favorable features of rough bottoms. The very stability of the larger-sized materials protects the bottom from washing, and may save the mussels from being smothered or carried away. It is of advantage to mussels to be surrounded by numerous other animals, especially by the smaller ones, which furnish attraction to fishes and thus promote the reproduction of the mussel. Many of these small animals live attached to stones, thus giving added value to gravelly and rocky bottom. In gravels, too, the youngest mussels may be protected through inaccessibility to enemies, and as they grow older the resemblance to small pieces of stone among which they lie may be the cause of escape from enemies. As previously indicated (p. 97), where bowlder rock or cobblestone bottoms occur in regions of rapids, mussels are commonly found abundantly and occur over the entire river.

The following table (6) embodies the experience of several observers regarding the preferences exhibited by 62 common species of fresh-water mussels for bottoms of different characters. In view of the intergradation of the several types of bottom and the almost unlimited variety of mixtures of sand, gravel, mud, and clay, the classification of the bottoms for the purpose of a table must of necessity be rough, and the characterization of mixed bottoms may in some cases be affected by the personal equation of the observer. Young mussels may have bottom requirements somewhat different from those of adults.

EXPLANATION OF TABLE 6.

The letters refer to the experience of the several observers (including the present authors and three previous writers), as follows: A, Baker (1898); B, Call (1900); C, Clark; D, Howard; E, Scammon (1906); F, Shira; G, Coker.

The use of large capitals indicates that, according to the observer whose letter is in large capitals, a certain type of bottom is preferred by the particular species of mussel. Wherever a small capital is used, the observer corresponding to the letter has indicated the type of bottom as favorable for the particular species of mussel, but not necessarily preferred to other favorable bottom.

The observations of Shira refer largely to lake conditions (Lake Pepin, Lake Pokegama, and Caddo Lake).

The observations of Coker refer primarily to shallow rivers (Grand River, Mich.).

The habitats indicated by Howard are based chiefly on the observed preferences of juvenile mussels in rivers, streams, ponds, and slues to the exclusion of true lakes.

TABLE 6.—HABITATS OF CERTAIN FRESH-WATER MUSSELS, CLASSIFIED ACCORDING TO CHARACTER OF BOTTOM.

Scientific name.	Common name.	Sand.	Sand and gravel.	Gravel.	Stones and rocks.	Mud and sand.	Mud and gravel.	Soft mud over firm bottom.	Mud.	Deep, soft mud.	Clay and sand.	Clay.
1. Alasmidonta calceola	Slipper-shell		D		G	D			A		C	
2. Alasmidonta marginata	Elk-toe	G	DG	BCG				c	A			
3. Anodonta corpulenta	Slop-bucket					F		c	FD	C		
4. Anodonta grandis	Floater					C		C	ABDE	c		
5. Anodonta imbecillis	Paper-shell	E				CF		C	AEF	D	c	
6. Anodonta suborbiculata	do.								BE	CD		
7. Anodontoides ferussacianus.		G	GD			DGC	G		A		C	
8. Arcidens confragosus	Rock pocketbook			D		c			BD	C		
9. Cyprogenia irrorata	Fan-shell			C								
10. Dromus dromas	Dromedary mussel		c	C								
11. Hemilastena ambigua				BC	ABD				B			c
12. Lampsilis alata	Pink heel-splitter	F				DF		C	ABEF	c	c	G
13. Lampsilis anodontoides	Yellow sand-shell	EGD				Dc		C	ABED			
14. Lampsilis capax	Pocketbook	C				D			D			
15. Lampsilis ellipsiformis		G		DG	GD				AE		C	
16. Lampsilis fallaciosa	Slough sand-shell	CF		DF		F		C	DF		c	c
17. Lampsilis glans				c				C				
18. Lampsilis gracilis	Paper-shell	EFG	F	D	D	F			ABDEF	C		G
19. Lampsilis higginsii	Higgin's eye	F	D	F							C	
20. Lampsilis iris	Rainbow-shell	AG	C	c	CG	DG		c	A			
21. Lampsilis lævissima	Paper-shell	EF				F		C	EF	cD		
22. Lampsilis ligamentina	Mucket	DGF	CFGD	cFG	DG		G	c	ABD		C	c
23. Lampsilis ligamentina gibba.	Southern mucket		C									
24. Lampsilis luteola	Fat mucket	CDFG	CF	DF				c	AEFD		c	
25. Lampsilis multiradiata		AC	C						A		c	
26. Lampsilis parva		D		D		D		C	ADEF			
27. Lampsilis purpurata	Purply	F	F			F				E		
28. Lampsilis recta	Black sand-shell	GF	D	EFG		F			AE		c	C
29. Lampsilis subrostrata		c							BED	C		c
30. Lampsilis ventricosa	Pocketbook	cFG	CGF	D	G	DF	G	c	DAE	D	c	
31. Margaritana monodonta	Spectacle-case	D	CD	Bc	BD			c	BD			
32. Obliquaria reflexa	Three-horned warty-back.	BDFG	FD	BCDFE	BD	D		c	ABD		C	c
33. Obovaria ellipsis	Hickory-nut	CDFE	cFD	cDF		D	D	c	D		c	
34. Plagiola donaciformis		CFDE	CDF	cDF		D	DF		ADE			
35. Plagiola elegans	Deer-toe	CEGF	CDF	CF	D				ADEF			
36. Plagiola securis	Butterfly	BDEF	F	BDECF		D		c	B		c	
37. Pleurobema æsopus	Bullhead		D					C	D		c	
38. Ptychobranchus phaseolus.	Kidney-shell										C	
39. Quadrula coccinea	Flat niggerhead		cDG	EG	GD	G				A	C	
40. Quadrula cylindraca	Rabbit's foot		c	C								
41. Quadrula ebenus	Niggerhead		DF	FGD	D	D		C				
42. Quadrula granifera	Purple warty-back		F	F				C				
43. Quadrula heros	Washboard		DF			F		c	BDF			C
44. Quadrula lachrymosa	Maple-leaf	AEG	D	E	c	DF		C	ABFE		c	c
45. Quadrula metanevra	Monkey-face		DF	BDCEF	D	D	D	c	BD			
46. Quadrula obliqua	Ohio River pig-toe		c								C	
47. Quadrula plicata	Blue-point	F	DF	F		DF		C	AB	cE		
48. Quadrula pustulata	Pimple-back	CD		c		D		c	BF			
49. Quadrula pustulosa	do.	FG	DF	CEF	D	F		C	ABFDE		c	
50. Quadrula rubiginosa		BGG	DG	B	BDG	DE	G	c	ABD		C	
51. Quadrula trapezoides	Bank-climber								FD			
52. Quadrula tuberculata	Purple warty-back	G		BC				c	ABF			
53. Quadrulata undata	Pig-toe	DF	DF	BDF	D	D		C	ABDF		c	
54. Quadrula undulata	Three-ridge	G	CG	G	G	D			AD	CG		G
55. Strophitus edentulus	Squaw-foot	CDGF	GDF	CDFG	G	DFG	G	c	ADEF		C	
56. Symphynota complanata	White heel-splitter	F	F	F		F		c	ABDEF	C		
57. Symphynota compressa			G							D	C	
58. Symphynota costata	Fluted shell	GF	CDGF	BCF	D	G			ADF		c	
59. Tritogonia tuberculata	Buckhorn	F	EF	DEF		F		C	BFDE		c	
60. Truncilla sulcata	Cat's paw		c								C	
61. Unio crassidens	Elephant's ear					F		C	BF		c	c
62. Unio gibbosus	Lady-finger	DFG	GF	DFGE	G	F	G		ADEF			

It appears from this and the following table that the preferred bottom for the majority of species is mud (but not deep, soft mud, to which type of bottom few species are adapted) and gravel, including sand and gravel. Sand ranks next and clay last; but few species of mussels exhibit a preference for sand or sandy clay, and only two are recorded (by one observer) as finding the most favorable environment in a bottom of clay unmixed with sand.

Table 6 may be simplified by reducing the types of bottom to four general classes, sand, gravel, mud, and clay, and by eliminating all but the leading commercial species. The results are indicated in Table 7 following:

TABLE 7.—PREFERRED HABITATS OF LEADING ECONOMIC FRESH-WATER MUSSELS, ACCORDING TO CHARACTER OF BOTTOM.

[X indicates preference as noted by majority and x by minority of observers.]

Scientific name.	Common name.	Sand.[a]	Gravel.[b]	Mud.[c]	Clay.[d]
Lampsilis anodontoides	Yellow sand-shell			X	
Lampsilis fallaciosa	Slough sand-shell			X	
Lampsilis recta	Black sand-shell	x	X	x	x
Lampsilis ligamentina	Mucket		X	x	x
Lampsilis ligamentina gibba	Southern mucket		X		
Lampsilis luteola	Fat mucket	X		x	
Lampsilis ventricosa	Pocketbook	X	x	X	
Obovaria ellipsis	Hickory-nut	X	x		
Plagiola securis	Butterfly		X	x	
Quadrula coccinea	Flat niggerhead		X	x	x
Quadrula ebenus	Niggerhead		X	x	
Quadrula heros	Washboard			X	x
Quadrula lachrymosa	Maple-leaf	x		X	
Quadrula metanevra	Monkey-face		X	x	
Quadrula obliqua	Ohio River pig-toe				X
Quadrula plicata	Blue-point		x	X	
Quadrula pustulosa	Pimple-back	x	x	X	
Quadrula rubiginosa		x		X	x
Quadrula undata	Pig-toe		x	X	
Quadrula undulata	Three-ridge		X	x	
Unio crassidens	Elephant's ear			X	
Unio gibbosus	Lady-finger		X	x	

[a] Sand alone.
[b] Including sand and gravel, mud and gravel, and rocks.
[c] Mud alone.
[d] Including sand and clay, mud and clay.

DEPTH.

The distribution of many animals of the water is known to be influenced by depth, the effect of which may be felt, among other ways, through pressure, light, temperature, dissolved gases, and freedom from wave action, or exposure thereto. In an indirect way, too, the effect of depth is experienced by any animal through the influence of these conditions upon food and enemies.

The increase of pressure is approximately 1 atmosphere for each 10 meters (33 feet) in depth, but fresh-water mussels are, so far as known, restricted to shallow waters where pressures must be insignificant. The Sphæriids are the only mollusks found below the 25-meter line in Lake Michigan (Shelford, 1913). Maury (1916, p. 32), (see Baker, 1918, p. 155), reporting the results of dredging in Cayuga Lake, N. Y., says: "These dredgings proved conclusively that Mollusca after 25 feet become very scarce. * * * In the greater depths no signs of Mollusca or of plants were found." In clear water minor depths do not markedly affect the light, but if the water is turbid, a common condition in the environment of fresh-water mussels, the penetration of light is very much diminished (see p. 114), and mussels if affected by light may, therefore, be expected to live at greater depths in clear lakes than in turbid streams. Temperature changes due to depth alone are so inconsiderable for shallow water as doubtless to have little effect upon the distribution of mussels, except where freezing to the bottom may occur.

The depth of water below which waves would reach them is apparently a factor in determining the habitat of many species of mussels in lakes (Headlee, 1906, p. 308—Winona Lake; Muttkowski, 1918—Lake Mendota). In large bodies of water like Lake Michigan the action of the waves is said to extend to 8 meters below the surface. The zone of wave action is a region in lakes comparable to the rapids and riffles of streams, where there is maximum circulation and aeration and a solid bottom suitable for such mussels as can withstand the violent action of waves and undertow currents. The species occupying this zone are given by Headlee for Winona Lake as the spike, *Unio gibbosus*, and the fat mucket, *L. luteola*. Baker (1916) says of this habitat in Oneida Lake:

> The shore may be free from vegetation. It receives the full force of the winds and waves from the open lake. The water is from 1 to 3 feet in depth and the bottom is heavily and thickly covered with stones and bowlders, many of the latter being of large size. Animal life is abundant, the clams living between the stones and on the sand between the stones.

The mussels he reported are as follows: *Elliptio complanatus*, common; *Lampsilis luteola*, rare; *Lampsilis radiata*, common; *Lampsilis iris*, rare; *Margaritana margaritifera*, rare; *Anodonta cataracta*, common; *Anodonta implicata*, common; *Anodonta grandis*, common; *Strophitus edentulus*, rare. Some of these are very thin shelled and doubtless survive the force of the waves only through the protection afforded by the large rocks. No doubt the thorough aeration of the water, resulting from wave action, is a favorable factor in this zone

On the shores of Lake Pepin one of the authors has often picked up live mussels that had been thrown up by heavy wave action. The mussels thus most frequently encountered were *Unio gibbosus*, *Lampsilis alata*, *Anodonta corpulenta*, *Strophitus edentulus*, *Lampsilis ventricosa*, and *Lampsilis luteola* in about the order named. They were usually immature examples. Occasionally after a storm had subsided one could see mussels that had not been entirely stranded on the beach near shore and in the act of making their way back again into deeper water. Headlee and Simonton (1904, p. 175) recorded similar observations.

While the data available are sufficient only to suggest how depth may affect the habitat selection of mussels, it is of interest to note some of the observations on this relation. A maximum depth of 22 feet for mussels in Winona Lake is given by Headlee (1906), who ascribes the control of distribution to bottom characters chiefly. Baker (1918) found that in Oneida Lake twice as many mussels occurred in water deeper than 6 feet as within the 6-foot contour. (See quotation, p. 103, above.) He records three species as limited to a depth of 1½ to 8 feet, three as living at varying depths between 1½ and 18 feet, and one subspecies as occurring only between 8 and 18 feet, the greatest depth which he explored. He reports an interesting case of bathymetric distribution of two races, *Lampsilis radiata*, occurring at 1½ to 3 feet, and a subspecies, *Lampsilis radiata oneidensis*, living only at 8 to 18 feet, the two forms showing a distinct difference in habitat. For Lake Mendota the optimum depth for mussels of the genera Anodonta and Lampsilis is given as from 2 to 3 meters (6 to 10 feet) (Muttkowski, 1918, p. 477); they were, however, found abundantly between 3 and 5 meters and rarely at greater depths than 7 meters (23 feet).

Wilson and Danglade (1914), in reporting a reconnoissance of mussel resources in Minnesota waters, give depths of the lakes, but without detailed data on the distribution of the mussels. In Lake Maxinkuckee, Evermann and Clark (1918, p. 255) say: "Mussels are to be found almost anywhere in water 2 to 5 or 6 feet deep where the bottom is more or less sandy or marly." Headlee (1906, p. 306) found that the mussel zone generally extended from the shore line to where the bottom changes from sand, gravel, or marl to very soft mud, a region in Winona Lake covered by from 4 inches to 9 feet of water. He did find, however, some mussels on sandy bottom in 22 feet of water. He made some experiments in retaining mussels at various depths and in a crate placed in 85 feet of water; only 1 of 10 specimens died in six days of exposure. After 12 days several specimens were found badly choked with mud.

In Lake Pepin mussels are plentifully found at depths ranging from 8 to 20 feet, but the majority are taken at depths ranging from 12 to 18 feet. Relative to the juvenile mussels, out of a total of 1,397 collected in 1914, 1,283, or 91.8 per cent, were taken at a depth of 3 to 8 feet; 2.6 per cent at 8 to 12 feet; 2.3 per cent at 12 to 16 feet; 0.4 per cent at 16 to 20 feet; and 2.9 per cent at 20 to 25 feet. *A. imbecillis* was the only juvenile found in any abundance at a depth greater than 15 feet, and 41 of the 79 individuals of this species collected were taken at 25 feet (Shira, report in manuscript).

A marked distribution with regard to depth has been observed in the artificial ponds at Fairport, Iowa. Here the species, *Lampsilis luteola*, is seldom found below a depth of 3 feet. When held in crates below this depth it does not thrive, although in its natural habitat, Lake Pepin, this species is abundant at a depth of 8 to 20 feet and has been taken at a depth of 25 feet.

In rivers and smaller streams mussels seem to be found commonly at lesser depths than in lakes, but unfortunately we have very few reports of observations in the deeper parts of large rivers. In the Illinois River, Danglade (1914) mentions a small bed 2 to 3 acres in extent above the mouth of Spoon River, where the bottom was of mud, the current about 2 miles per hour, and the depth of water 8 feet. At Chillicothe he found a good bed at a depth of 12 to 15 feet. The survey of Andalusia Chute, Mississippi River (Howard, report in preparation), carried on during relatively high-water stages in 1915, revealed no mussels in the deeper portion of the river over 12 feet in depth, and the greater number of mussels were found at depths less than 10 feet. Local informants at Madison, Ark., stated that the niggerhead, *Quadrula ebenus*, was found in water 20 to 50 feet deep; it was also said that in flood season it was captured from a depth of 75 feet. There has been no opportunity, however, to verify these statements.

With regard to a collection of 183 juveniles of the Quadrula group from 12 stations in the Mississippi River, Howard (1914, p. 34) reported depths from 0 to 8 feet. Wilson and Clark (1914) reported a rich find (19 species) in the Rock Castle River off the Cumberland, in water having a maximum depth of 1½ feet. In the Grand River, Mich., the senior author has found mussels (muckets, *Lampsilis ligamentina*, three-ridge, *Quadrula undulata*, and others) in conspicuous abundance in swift water less than a foot in depth. Boepple (Boepple and Coker, 1912) found mussels abundant and of fine commercial quality in water from 1 to 3 feet in depth in the Holston and Clinch Rivers of Tennessee. In Caddo Lake, Tex., Shira (1913) found an abundance of mussels in 4 to 8 inches of water, and in many places there was scarcely enough water to cover the shells. This lake was very shallow over large areas. In fact, mussels are frequently found in very shallow water where the conditions of the bed of the stream and other factors are favorable. In various parts of the country considerable commercial quantities of mussels are collected by hand from shallow waters. At one such place, Lyons, Mich., the mucket, *Lampsilis ligamentina* comprised 80 per cent of the collection, although the three-ridge, *Quadrula undulata*, the pocketbook, *Lampsilis ventricosa*, the spike, *Unio gibbosus*, and the black sand-shell, *Lampsilis recta*, were quite common. Among other species that were frequently found in very shallow water (1 to 2 feet in depth) in that stream were the following: *Lampsilis luteola*, *iris*, and *ellipsiformis*, *Quadrula coccinea* and *rubiginosa*, *Strophitus edentulus*, *Symphynota compressa* and *costata*, *Alasmidonta marginata*, *Anodontoides ferussacianus*, and *Anodonta grandis*. ·In fact, the only species that were not found in water less than 6 feet in depth in the Grand River were the three-horned warty-back, *Obliquaria reflexa*, the hickory-nut, *Obovaria ellipsis*, the deer-toe, *Plagiola elegans*, and the white heel-splitter, *Symphynota complanata*.

LIGHT.

The small floater, *Anodonta imbecillis* Say, in sunlight will draw in its siphons when a shadow passes over. Wenrick (1916) has demonstrated experimentally with measured illumination, that a fresh-water mussel, *Anodonta cataracta* Say, is very sensitive to decrease in intensity of light. Observations in the Washington laboratory indicate that the yellow sand-shell, *Lampsilis anodontoides*, will close when a black cloth is placed over the aquarium, but will open when exposed either to daylight or to the light of a bright electric lamp. These reactions may be for protection of the animal from approaching enemies, but it is probable also that the distribution of mussels is largely influenced by light conditions. Mussels are seldom found in vegetation which is dense enough to exclude the light to a great extent. This is especially true with regard to plants like the water lily which have floating leaves. Some relations to vegetation are brought out in a study of the habitats in Oneida Lake (Baker, 1916).

An exceptional case is reported by Wilson and Danglade (1914, p. 15) where the mussels were found in densest aggregation submerged deeply in the bottom and below a covering of vegetation. Their account is of sufficient interest to be quoted in full:

> The bottom of the river where these shells are obtained is covered with algæ and water weeds to the depth of 12 to 18 inches, and the thicker the vegetation the more plentiful the mussels beneath it. Two men were actively working the Shell River at Twin Lakes near Menahga at the time of our visit, and we watched them rake off the algæ and weeds and then dig into the underlying gravel and sand for the mussels. The latter are often buried to the depth of a foot or more. This is, at the least, a novel condition and one which, so far as is known, has not been reported from any other locality.

Certain species of mussels, the mucket, pocketbook, black sand-shell, and others are sometimes pink-nacred and sometimes white-nacred, and with the two former, at least, the outside covering of the shell has a reddish cast in pink-nacred examples. With such species it is a matter of common observation that pink-nacred shells and brightly colored exteriors are more frequently found in shallow clear water where the mussels are exposed to bright light.[a] Thus the black sand-shells of the upper part of the Grand River, Mich., have a deep purple nacre, while white shells of the same species predominate in the more turbid Mississippi. The spike, *Unio gibbosus*, is usually purple-nacred, but uncommon examples that are nearly white are found in turbid rivers. Clark and Wilson (1912) describe the Maumee River as rather muddy most of the time, and it is interesting to find that they report that two-thirds of the spikes, *Unio gibbosus*, in that river were white-nacred and that the black sand-shells were usually white-nacred.

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[a] Grier (1920a) presents the result of an extensive study of the nacreous color of mussels. He notes a tendency to lighter or bluish nacreous color in the lower portion of stream courses. He has evidence of some correlation between color and sex.

The reputed migration of certain mussels toward shore in time of flood may be an accommodation to light conditions associated with turbidity of water under such conditions. We have virtually no data on the distribution of mussels with respect to permanently shaded areas or with regard to the reactions to daily changes in light.

CURRENT.

The luxuriant development of certain mussels in streams where the current is strong, in contrast with their growth in sluggish portions of rivers and lakes, bears witness to the significance of current as a favorable factor of environment for fresh-water mussels. Current is a characteristic feature of streams, and the rate of flow is largely determined by the gradient of the channel. Currents producing a circulation of water occur also in lakes, where they are caused chiefly by wind and to a less extent by changes of temperature. In some lakes the circulation extends from top to bottom, but in small deep lakes only a partial surface circulation commonly prevails (Birge and Juday, 1911). Undertow currents are also developed where there is wave action, and under some conditions convection currents must exist in natural bodies of water, but we have little data on this.

Shelford (1913) emphasizes the relation of water animals to current as follows:

> The distribution of dissolved salts and gases is dependent upon the circulation of the water, as their diffusion is too slow to keep them evenly distributed. The water of streams has been found to be supersaturated with oxygen [citing Birge and Juday, 1911]. Oxygen is taken up by water near the surface. Nitrogen and carbon dioxide are produced especially near the bottom, and if the water did not circulate they would be too abundant in some places and deficient in others for animals to live (p. 60). * * *
>
> The current in streams differs from that in lakes in that it is for the most part in one direction while the lake currents often alternate. There are backward flows and eddies at various points in streams in front of and behind every object encountered in the current. As we pass across a stream we find the current swiftest near the surface in the middle and least swift at the bottom near the sides (p. 61). * * *
>
> The factors of greatest importance in governing the distribution of animals in streams are current and kind of bottom. They influence carbon dioxide, light, oxygen content, vegetation, etc. (p. 66).

Since mussels are bottom dwellers and largely stationary in habit, one can appreciate how dependent they must be upon circulation of the water to bring renewed supplies of organic food, mineral matter in solution, and oxygen, and to remove the poisonous products of metabolism that are produced in their own bodies and in those of other organisms living about. Mussels, of course, cause by their respirative currents circulation of the water immediately about them, but this is not sufficient to prevent an early exhaustion of food supply unless broader currents prevail.

It must be emphasized, too, that flowing water carries more matter in suspension than still water. It has been seen (p. 91) that the food of mussels consists to a considerable extent of the finely divided solid matter; but such materials, however abundant on the bottom, are not available to the mussel until they are taken up in the water and carried to the mussel. The effects of the current, then, both in lifting solid matter from the bottom and in holding it in suspension play a foremost part in its relation to the welfare of mussels. The power of water to move solid matter on the bottom increases very rapidly with the rate of flow.

The capacity of water to move solid matter from a condition of rest on the bottom of a stream varies with the sixth power of the velocity of the stream. If the velocity is doubled, the increase in the force which is capable of putting the particle in motion is multiplied 64 times. (New York report of Metropolitan Sewerage Commission, 1912, p. 41.)

Fish frequent areas near the current but maintain themselves in eddies or in places where the current is relatively slack, as at the bottom and near the shores (Shelford, 1913). In view of the essential part that fish play in the distribution of mussels, the habits of the fish may be a very significant factor in the distribution of mussels with reference to current. It has been suggested by Evermann and Clark (1918, p. 252) that currents may promote the reproduction of mussels by making fertilization of the egg more certain and by decreasing the chance for inbreeding through the conveyance of sperm from mussels farther upstream. In still waters the chance for fertilization of eggs may be less favorable.

The relations of mussels to temperature have not been fully investigated, but it seems certain that flowing water must protect mussels from excessively high temperatures and thus permit many species to live in much shallower water in streams than in ponds or lakes.

The tendency of mussels to locate apart from the main channel and nearer the banks of the streams has previously been mentioned (p. 97). While this distribution may be partly due to the fact that there the full force of the current is avoided while many of its benefits are received, nevertheless it must not be overlooked that many species of mussels thrive in rapid shallow streams and that such regions of swift water in the Mississippi River, as the former "rapids" at Keokuk or the existing "rapids" above Davenport, have been among the most prolific mussel grounds of the entire river. In these circumstances, however, the rocky nature of the bottom affords the mussels protection against some effects of the current. Evidently the barrenness of the main channel in most cases is due rather to the nature of the bottom combined with the force of flow than to the strength of current alone.

On page 99 there have been listed the species of mussels which are characteristic of lakes and ponds, regions of comparatively still water. The more common mussels of rivers may be classified according to apparent adaptation to sluggish water, strong current, and rapids (Table 8). These general comments should be made: In a firm bottom, such as furnishes good anchorage, a mussel may dwell in a current swifter than is characteristic of its common habitats; where rocks furnish shelter, mussels below them may be in rather slow water despite the current around them; deep water may be fairly sluggish under a swift surface current.

EXPLANATION OF TABLE 8.

The symbols are those used in Table 6, C representing Clark; D, Howard; F, Shira; and G, Coker. The large capital denotes preference in the opinion of the observer, for a particular condition of current. The small capital denotes that the condition is favorable but not, so far as is known, preferred to other conditions. When no large capital occurs on a line, no preference is indicated; and when a particular letter appears in small capital throughout a line, the observer denoted by the letter has no evidence upon which to base an opinion of discrimination on the part of the particular mussel between the different conditions of current regarded as favorable.

TABLE 8.—CLASSIFICATION OF COMMON FRESH-WATER MUSSELS IN RELATION TO CURRENT.

Scientific name.	Common name.	Little or no current.	Fair or good current.	Strong or swift current.
1. Alasmidonta calceola	Slipper-shell		CG	
2. Alasmidonta marginata	Elk-toe		C	DG
3. Anodonta corpulenta	Slop-bucket	CDF	cf	
4. Anodonta grandis	Floater	CDF	cg	
5. Anodonta imbecillis	Paper-shell	cDF	cf	
6. Anodonta suborbiculata	do	CD		
7. Anodontoides ferussacianus		cg	Cg	g
8. Arcidens confragosus	Rock pocketbook	CDF		
9. Cyprogenia irrorata	Fan-shell			C
10. Dromus dromas	Dromedary mussel			C
11. Hemilastenia ambigua		D	Cd	
12. Lampsilis alata	Pink heel-splitter	cDFG	cf	
13. Lampsilis anodontoides	Yellow sand-shell	d	CDF	
14. Lampsilis capax	Fat pocketbook	cD	C	
15. Lampsilis ellipsiformis		cg	CG	D
16. Lampsilis fallaciosa	Slough sand-shell	DF	Cf	
17. Lampsilis glans		c	c	
18. Lampsilis gracilis	Paper-shell	CDFG	cdf	
19. Lampsilis higginsii	Higgin's eye		CDF	
20. Lampsilis iris	Rainbow-shell	cgD	CG	
21. Lampsilis lævissima	Paper-shell	CDF	f	
22. Lampsilis ligamentina	Mucket		CF	DG
23. Lampsilis ligamentina gibba	Southern mucket		C	c
24. Lampsilis luteola	Fat mucket	CDFG	cfg	
25. Lampsilis multiradiata			c	C
26. Lampsilis parva		CDF		
27. Lampsilis purpurata	Purply	cF	cf	
28. Lampsilis recta	Black sand-shell	f	CDFG	g
29. Lampsilis subrostrata		CD	c	
30. Lampsilis ventricosa	Pocketbook	cfgd	cdFG	g
31. Margaritana monodonta	Spectacle-case		CD	
32. Obliquaria reflexa	Three-horned warty-back	df	CFGd	d
33. Obovaria ellipsis	Hickory-nut		CDFG	
34. Plagiola donaciformis		df	CDF	
35. Plagiola elegans	Deer-toe	f	CFG	D
36. Plagiola securis	Butterfly	d	CDF	
37. Pleurobema æsopus	Bullhead		CDF	
38. Ptychobranchus phaseolus	Kidney-shell		C	
39. Quadrula coccinea	Flat niggerhead		CDg	dG
40. Quadrula cylindrica	Rabbit's-foot		CF	
41. Quadrula ebenus	Niggerhead		CFd	D
42. Quadrula granifera	Purple warty-back		Cd	D
43. Quadrula heros	Washboard	df	CDF	
44. Quadrula lachrymosa	Maple-leaf	DF	CFG	
45. Quadrula metanevra	Monkey-face	f	CDF	d
46. Quadrula obliqua	Ohio River pig-toe		C	
47. Quadrula plicata	Blue-point	cdf	CDF	
48. Quadrula pustulata	Pimple-back	cd	CDF	c
49. Quadrula pustulosa	do		CFGd	D
50. Quadrula rubiginosa		cg	CDG	dg
51. Quadrula trapezoides	Bank-climber	cF	cf	
52. Quadrula tuberculata	Purple warty-back		cg	cg
53. Quadrula undata	Pig-toe	Df	CFd	
54. Quadrula undulata	Three-ridge	cgD	CFGd	G
55. Strophitus edentulus	Squaw-foot	cgDF	cdg	
56. Symphynota complanata	White heel-splitter	cfg	CDF	
57. Symphynota compressa			g	g
58. Symphynota costata	Fluted shell		CF	d
59. Tritogonia tuberculata	Buckhorn	dfg	CFd	Dg
60. Truncilla sulcata	Cat's paw		C	
61. Unio crassidens	Elephant's ear		CDF	
62. Unio gibbosus	Lady-finger	cdgF	cdg	DG

WATER CONTENT.

The matter that is carried in all natural waters in varying quantities and proportions consists of suspended matter, both dead and living, minerals and other ordinarily solid substances in solution, and dissolved gases. All of these classes of substances are utilized by fresh-water mussels in one way or another, and the quantity of any of them in the water has a direct bearing upon the suitability of waters for mussels.

SUSPENDED MATTER.

The solids carried in suspension by water consist of mineral and organic substances. The particles of mineral matter brought in by surface drainage or derived from bottom and shores, apart from that which is in solution, range in size from coarse to very minute. The carrying power of the water varies with the sixth power of the velocity, although in the case of the most minutely divided substances other factors than rate of flow come into play.

Mussels are affected in various ways by the matter in suspension. It has been reported that some mussels stop feeding when the water is excessively turbid, as after a storm. In this way they would avoid taking into their stomachs large amounts of indigestible mineral. They have, however, the power of ejecting undesirable matter; this may enable them to continue feeding even though the water is moderately turbid In streams like the Mississippi, mussels could hardly survive without feeding during the long periods of turbidity that prevail. Excessive precipitation of silt may smother or even bury the mussel (Headlee and Simonton, 1904, p. 176). The turbidity of water over deeper beds materially restricts the amount of light reaching the mussel, and it is possible that this has an untoward effect. Data regarding the turbidity of several streams are given in Table 9, page 116. The turbidity of representative mussel-producing streams varies from 37 to 188, except that the Des Moines River at Keosauqua has a turbidity rating of 542—a striking exception. The Missouri and Red Rivers (non-productive) and portions of the Mississippi River which do not yield commercial mussels have turbidity ratings from 556 to 1,931.

Organic materials, both living and dead, are abundantly suspended in most natural waters, and form a large part of the food of mussels. (See p. 91.) The living bodies are the microscopic plants and animals which make up what is called the plankton. The dead organic materials are the remains or fragments of plants and animals in a state of decomposition, and such also form a part of the food supply.

Some of the plankton originates in the lake or stream in which the mussels are living. Another and perhaps the greater part is brought in by the tributary streams. Similar statements may be made regarding the dead organic matter, with the addition that some of this may be brought in by surface drainage from the bordering lands.

MINERALS IN SOLUTION.

To what extent mussels derive the mineral matter necessary for the sustenance of life and the formation of shells directly from the water or through the solid food consumed can not be said, but even that part which is derived from solid food must have been obtained by the smaller organism from the water or the soil. Churchill (1915 and 1916), from experiments conducted at the Fairport Station, has shown that fresh-water mussels possess the ability to make use of nutriment which is in solution in the water. While he demonstrated this for such nutritive substances as fat, protein, and starch, there are yet wanting, as he has pointed out, analyses of the natural water in which mussels live to prove that such organic substances are present in the waters in quantities sufficient to play an important part in the nutrition of mussels. There are, however, abundant analyses to prove the presence of dissolved minerals.

The requirements of mussels in mineral food may be ascertained by analysis of the soft bodies and shells. Such analysis shows that while the shell is about 95 per cent calcium carbonate, and 3½ per cent organic matter, it also contains other minerals in very small proportions, less than 1 per cent each, such as silica, manganese, iron, aluminum, and phosphoric acid. It does not follow that because these minerals, other than calcium, occur in minute proportions, they are any the less essential to the welfare of the mussel; iron forms a very small proportion of the human body, but man can not live without it. So these minerals may, then, be just as essential to the formation of good shell as calcium, but with the possible exception of manganese it is probable that all natural waters contain a sufficient quantity of the minerals to satisfy the needs of mussels. Nevertheless an interesting and important problem may be found in a comparative study of the mineral content of different waters which yield shells of diverse qualities. It is even possible that an excessive proportion of certain minerals in water tends to the formation of shells that are brittle, discolored, or otherwise inferior.

The sundried meats of mussels from the Mississippi River when analyzed have been found to contain, besides moisture (about 7.6 per cent), protein (calculated from nitrogen), 44 per cent; glycogen, about 9 per cent, ether extract (presumably fats), a little less than 3 per cent; and undetermined organic material, 13 per cent. The remainder is mineral matter (chiefly phosphoric acid), 9 per cent; calcium (calcium oxide), 8 per cent; silica, 3½ per cent; manganese, about one-half of 1 per cent; and such other minerals in small proportions as sodium, potassium, iron, and magnesium (Coker, 1919, p. 62, analysis by U. S. Bureau of Chemistry).

As previously indicated, nearly all natural waters, at least those fed largely with surface drainage, probably contain certain quantities of the required minerals, but it would be going beyond the bounds of present knowledge to say whether or not the abundant growth of mussels in certain streams and the variable qualities of shells produced in different streams are related to the proportions of minerals present other than calcium. Certain it is that a deficiency of lime is very unfavorable. The soft waters of the Atlantic slope support very few mussels and these are small in size and possess thin shells which are usually badly eroded. The thinness of the shells is associated with the deficiency of calcium in the water, and the erosion is an indirect result of the same cause, since the free carbonic acid, which attacks and consumes the shells wherever the protective horny covering has been broken by abrasion, would, in harder waters, be combined with the calcium in solution to form the bicarbonate.

Circulation, of course, plays a great part in making available to mussels the dissolved content of the water. It may be due not so much to low calcium content as to inadequate circulation that small lakes and ponds in States of the Middle West generally yield mussels with thin or dwarfed shells.

The waters of many streams of the United States have been subjected to analysis by the United States Geological Survey (Dole, 1909). The summarized analyses for several streams, or parts of streams, productive of mussel resources, and for 10 others that are not productive of commercial shells, are given in Table 9 below. It appears that, within broad limits, the variations in content of silica, iron, magnesium, sodium, and potassium are not significant as affecting productiveness (unless, as may be the case, the quality of the shell produced is affected). Particular attention may be directed to the columns of turbidity, calcium, carbonate radicle, and nitrate radicle. The nonproductive streams, or parts of streams, listed are generally either very high in turbidity or very low in calcium, bicarbonate, and nitrate. The Shenandoah, among nonproductive streams, is an interesting exception. So far as can be seen, its analysis conforms essentially to the standard of productiveness in mussels as revealed by streams of the Mississippi Basin. It is possible, then, that the Shenandoah, and perhaps a few other streams of the Atlantic or Pacific slopes, might support fresh-water mussels of commercial value should the proper species be introduced.

TABLE 9.—CONTENTS OF WATERS OF CERTAIN PRODUCTIVE MUSSEL STREAMS AND OTHER NONPRODUCTIVE STREAMS.[a]

	Turbidity.	Suspended matter.	Coefficient of fineness.	Total iron (Fe).	Silica (SiO_2).	Iron (Fe).	Calcium (Ca).	Magnesium (Mg).
PRODUCTIVE RIVERS.								
Wabash, Vincennes, Ind	172	193	1.20	....	13.0	0.24	61.0	22.0
Illinois, La Salle, Ill	159	136	.80	....	12.0	.21	50.0	22.0
Illinois, Kampsville, Ill	188	145	.80	....	12.0	.27	47.0	20.0
Fox, Ottawa, Ill	94	87	1.20	....	11.0	.20	60.0	32.0
Sangamon, Springfield, Ill	74	39	.80	....	16.0	.32	52.0	24.0
Cumberland, Nashville, Tenn	126	94	.74	....	20.0	.42	26.0	3.6
Cumberland, Kuttawa, Ky	176	165	.92	....	18.0	.30	28.0	4.3
Des Moines, Keosauqua, Iowa	542	642	1.09	....	22.0	.36	58.0	21.0
Grand, Grand Rapids, Mich	37	43	1.61	1.1	14.0	.07	56.0	19.0
Cedar, Cedar Rapids, Iowa	64	61	.97	....	14.0	.09	48.0	16.0
Maumee, Toledo, Ohio	143	112	.95	3.4	17.0	.27	57.0	16.0
Mississippi, Moline, Ill	117	106	.9	....	16.0	.39	33.0	13.0
Mississippi, Quincy, Ill	173	119	.8	....	18.0	.46	36.0	16.0
NONPRODUCTIVE RIVERS.								
James, Richmond, Va	90	71	.96	3.9	18.0	.5	14.0	3.0
Potomac, Cumberland, Md	28	29	1.59	3.0	8.2	.14	24.0	4.6
Wateree, Camden, S. C	259	214	.79	....	25.0	.28	6.3	1.8
Shenandoah, Millville, W. Va	31	39	1.64	.9	15.0	.08	32.0	8.2
Mississippi, Chester, Ill	858	634	....	.8	22.0	.39	44.0	16.0
Mississippi, Memphis, Tenn	556	519	.97	....	24.0	.61	36.0	12.0
Red, Shreveport, La	790	870	1.11	....	30.0	1.1	74.0	17.0
Missouri, Ruegg, Mo	1,931	1,890	1.02	....	29.0	.51	52.0	16.0
Savannah, Augusta, Ga	172	142	.77	....	23.0	.44	5.7	.8
Hudson, Hudson, N. Y	13	16	1.26	.7	11.0	.15	21.0	3.8
Cape Fear, Wilmington, N. C	73	21	.92	1.3	9.9	.78	5.0	1.5

	Sodium and potassium (Na+K).	Carbonate radicle (CO_3).	Bicarbonate radicle (HCO_3).	Sulphate radicle (SO_4).	Nitrate radicle (NO_3).	Chlorine (Cl).	Total dissolved solids.
PRODUCTIVE RIVERS.							
Wabash, Vincennes, Ind	25.0	0.0	230	55.0	6.4	36.0	336
Illinois, La Salle, Ill	16.0	....	203	50.0	6.6	13.0	278
Illinois, Kampsville, Ill	18.0	....	202	42.0	4.3	15.0	267
Fox, Ottawa, Ill	14.0	....	275	61.0	4.9	7.9	335
Sangamon, Springfield, Ill	16.0	....	247	37.0	3.4	7.5	276
Cumberland, Nashville, Tenn	9.6	.0	92	14.0	1.2	2.1	119
Cumberland, Kuttawa, Ky	7.8	.9	100	9.7	1.8	3.0	124
Des Moines, Keosauqua, Iowa	17.0	.0	216	71.0	3.3	4.8	312
Grand, Grand Rapids, Mich	10.0	8.5	214	33.0	2.3	7.7	258
Cedar, Cedar Rapids, Iowa	12.0	.0	209	30.0	3.1	3.4	228
Maumee, Toledo, Ohio	24.0	2.5	173	48.0	4.5	40.0	298
Mississippi, Moline, Ill	10.0	....	152	24.0	1.8	3.7	179
Mississippi, Quincy, Ill	11.0	....	175	25.0	2.2	4.4	203
NONPRODUCTIVE RIVERS.							
James, Richmond, Va	6.7	.0	60	7.1	.3	2.3	89
Potomac, Cumberland, Md	9.0	.0	36	58.0	.9	6.4	130
Wateree, Camden, S. C	8.4	.0	34	4.2	.4	2.8	73
Shenandoah, Millville, W. Va	6.7	1.3	132	6.2	2.6	3.0	140
Mississippi, Chester, Ill	21.0	....	174	56.0	2.7	9.8	269
Mississippi, Memphis, Tenn	19.0	.0	129	43.0	1.7	8.6	202
Red, Shreveport, La	90.0	4.6	135	140.0	.4	121.0	561
Missouri, Ruegg, Mo	36.0	.0	178	104.0	2.9	12.0	346
Savannah, Augusta, Ga	12.0	.0	30	6.0	.6	2.1	60
Hudson, Hudson, N. Y	7.9	.0	73	16.0	.8	4.0	108
Cape Fear, Wilmington, N. C	7.2	.0	25	3.2	.2	5.8	57

[a] After U. S. Geological Survey.

DISSOLVED GASES.

Air is inconspicuous, yet nothing is more important to man. Without it he dies; and his comfort, health, and normal development depend upon the purity of the air by which he is surrounded. This is because of the absolute necessity for oxygen, and the deleterious effect of too much carbonic-acid gas. The gases dissolved in water are as invisible as air, but the mussels are as dependent upon the free oxygen in solution in the water as man is dependent upon the oxygen of the air. The water of streams and lakes dissolves air at the surface from the atmosphere and derives it from the physiological action of plants in light. Cold water will hold more free oxygen than warm, but the absorption of oxygen at the surface is favored by increased evaporation, with warm dry air and the prevalence of winds (W. E. Adeney, in Report of the Metropolitan Sewerage Commission of New York, 1912, p. 81). Falls, rapids, and swift currents promote the absorption of oxygen, and circulation currents lead to its better distribution into the deeper parts and throughout the whole body of water. Even without the aid of circulation currents, a measure of distribution of oxygen dissolved at the surface is effected by diffusion and "streaming" of the gas within the water (W. E. Adeney, loc. cit., p. 82).

Carbon dioxide (CO_2), commonly called carbonic-acid gas, which is given off as a waste product of mussels and other animals, and which is also formed by the decomposition of animal and vegetable matter, is helpful in small quantities, but is poisonous to animals when present in too great quantities (Shelford, 1913, p. 59; 1918, pp. 39, 40; and 1919, p. 106). It is used up by green plants in sunlight and is also given off to the atmosphere at the surface of the water. The same conditions that are favorable to the absorption of oxygen are also favorable to the loss of CO_2.

Carbon dioxide is of especial significance sometimes because of its tendency to unite with calcium carbonate to form the bicarbonate, which is soluble in water. Since the shell of a fresh-water mussel is composed principally of calcium carbonate it is liable to be attacked by free carbon dioxide in the water and taken up into solution. The horny covering of the shell is a protection against the action of the gas, but if that becomes broken or worn off in spots, as frequently occurs, the shell is exposed to the destructive effect of the acid. This leads to little harm in hard waters where the CO_2 may unite with the calcium carbonate derived from rocks or soils, but in soft waters, or in any waters where there is an excess of gas over dissolved calcium, the shells are partially or completely destroyed by corrosion. On many rivers "baldhead" shells are commonly encountered, and sometimes the shells are full of pits or even eaten clean through in the older parts.

Nitrogen, though an important element in the composition of mussels, can not be used by them in the form of a gas, and its presence in water (unless in excess) is presumably a matter of indifference to them, just as the nitrogen which composes the bulk of the atmosphere is uninjurious to men and not directly utilized by them (Shelford, 1918, p. 36). Other gases found in water are ammonia, methane (CH_4) and other hydrocarbons, and hydrogen sulphide (H_2S), which are formed in certain processes of decomposition (Needham and Lloyd, 1916, p. 47). These are of importance only when occurring in sufficient quantity to be injurious.

Mussels and other animals grow more plentifully in regions of water where, with other conditions favorable, there is a proper gas content—abundant free oxygen and limited amounts of carbon dioxide. Such places are near zones of wave action in lakes and in rapids in streams, where the influence of green plants is felt, and where water circulation is good.

VEGETATION.

In many lakes and streams in protected locations rooted plants occur in more or less abundance. If this vegetation is of open character, not producing a heavy shade, it frequently harbors an extensive mussel fauna (Baker, 1916, pp. 94 and 95). This kind of habitat is especially favorable to many fishes,[a] and to this fact in part may be attributed the presence of mussels, since the young mussels upon leaving the fish, having small power of locomotion, will remain where they fall if the habitat is at all suitable. Since mussels are found in abundance where there is no vegetation, as in rivers like the Mississippi, and generally are conspicuously absent from dense growths, it would seem that the association with rooted plants is largely incidental. There is other direct evidence to indicate that mussels of such habitats are those that are parasites upon species of fish that have a preference for such an environment.

Shira's observations in Lake Pepin (unpublished manuscript) indicated a certain association of juvenile mussels and vegetation, since 94 per cent of the juvenile mussels taken in a survey conducted in 1914 were taken in situations where more or less vegetation was encountered. On the other hand, he found juveniles at as many stations without vegetation as with it. As the result of many observations he concluded that a dense growth of vegetation was distinctly unfavorable to the survival of young mussels, and he suggests that the association of juvenile mussels with vegetation may be partly due to the fact that environments marked by the presence of aquatic plants are attractive to fish. He also observed that a given area of bottom supportive of mussels might display a heavy growth of aquatic plants one year but be practically or entirely free of them in another year. The same author has observed relatively dense growths of vegetation on mussel beds in Lake Pokegama.

It has frequently been observed in lakes that mussels live abundantly in patches of Chara, a low-growing green plant usually containing a considerable proportion of calcium carbonate. In the Grand River, Mich., Coker noted that mussel collecting was invariably poor in the midst of abundant rooted plants. The principal species found in such localities were the floaters (*Anodonta grandis*), the fat mucket (*Lampsilis luteola*), and the pink heel-splitter (*Lampsilis alata*). The mucket (*Lampsilis ligamentina*), and other species were likely to be found in the vicinity of rooted aquatic plants.

As quoted on page 110, above, Wilson and Danglade (1914, p. 15) described the finding of mussels beneath layers of algæ and weeds in Minnesota streams.

It must be remarked that rooted plants are not the only ones that contribute to the oxygen supply and to the depletion of the carbon dioxide of the water. There are thread algæ and innumerable microscopic floating plants which play an important if not the most important part in oxygenation of the water, and these are widely distributed in all zones to which sunlight penetrates.

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[a] "Little fishes and the greater number of mature fishes keep more or less closely to the shelter of shores and vegetation" (Needham and Lloyd, 1916, p. 23).

ANIMAL ASSOCIATES.

In the previous discussion of the Naiades in relation to the physical environment, there has been shown to be an adaptation by certain species to particular physiographic situations, as to pond, lake, river, swift or quiet water, hard or soft bottom, etc. In any habitat each mussel is in association with other mussels of the same or other species and with animals and plants of various classes, all more or less adapted to the same environment. Such an association of organisms forms a community, the members of which interact more or less upon one another and upon their environment. The consideration of these communities with reference to their members and to the environment often reveals important relations. Because of the mutual relations existing, a disturbance or destruction of any one element, by affecting a balanced condition, may cause a marked disturbance of the whole community. (See Shelford, 1913, p. 17.) Some of the relations between mussels and their associates may be described as competition, symbiosis and commensalism, parasitism, and preying. A description of a typical habitat with its inhabitants will illustrate the variety of life associated with mussels. For Oneida Lake, N. Y., Baker (1916, p. 94) gives an account of a particular sort of habitat which he designates the bulrush-waterwillow type, where there is not great exposure to waves, where the bottom is more or less covered with stones and bowlders, but with sandy spots here and there, where the depth varies from 1 to 4 feet, and where the vegetation consists of bulrushes, waterwillows, and pickerelweed.

> The principal differences between this habitat and the bowlder type are the less exposed situation, the density of the vegetation, the deeper water, and the sandier bottom. Such a habitat is particularly favorable for black bass, sunfish, rock bass, and others, because of the hiding and breeding places provided by the thick vegetation, the attachment for eggs by the roots and stems of plants, and the excellent feeding ground, by the abundance of animal life, insect, crustacean, and molluscan. The largest number of molluscan species, 39, occur in this type of habitat, including upwards of 15 which are known to be eaten by bottom-feeding fish. [The following numbers of species are listed: Mussels, 11, including several species of Anodonta and Lampsilis; univalves, 16; crustaceans, 1 (crayfish); Sphæriids, 10; leeches, 5; insects, 4.]

A typical association of mussels and other species in Andalusia Chute, Mississippi River, near Fairport, Iowa, is as follows (Howard, unpublished notes):

Bottom—gravel, rock, and sand.
Water—depth 5½ to 7½ feet. Current at surface estimated 2 miles.
Haul—250 feet in length, with crowfoot drag 10 feet wide and with dredge 18 inches wide.
Distance from edge of water—20 feet.
Mussels—*Lampsilis gracilis*, 3; *Plagiola elegans*, 1; *P. donaciformis*, 3; *Quadrula ebenus*, 1; *Q. metanevra*, 3; *Q. pustulosa*, 1; *Q. undata*, 2; *Strophitus edentulus*, 1; and *Unio gibbosus*, 3. Total, 18.
Bivalve—*Musculium transversum* Say, 1.
Bryozoa—*Plumatella polymorpha* Kraepelin, 1 colony.
Snail—*Vivipara subpurpurea* Say, 36; *Pleurocera elevatum*, Say 1.
Flatworm—Planarian.
Leech—*Placobdella parasitica* Say.
Insects—Stonefly, Perla sp. (larvæ); mayfly, Chirotenetes, 1 (larva); Heptagenia, 14 (larvæ); Polymitarcys, 2; dragonfly, *Gomphus externus*, 5, Argia, 3 (larvæ), Neurocordulia, 1; caddisfly, Hydropsyche, 70 (larvæ); beetle, Parnids, 2 (adult).
Crustacea—Crayfish, Cambarus.

In communities of animals and plants, as the individuals increase in numbers there may develop the keen competition for food which has been designated as the struggle for existence of the animate world. Since mussels feed upon suspended matter, living or dead, which they filter from the water, and since water once filtered must be less richly supplied with food for other mussels, an actual competition for food undoubtedly exists. Clark and Wilson (1912, pp. 19–20) give an account of a measured area of 1 square meter (10.76 square feet) in which they counted 81 mussels and 57 other mollusks, making a total of 138 individuals, or about 13 per square foot; and there were present, of course, many other animals, some of which took the same kind of food as the mussels. This recorded determination of numbers per given area illustrates the possibilities of competition. As indicated on pages 91 and 93, above, a detrimental competition for organic food probably does not occur ordinarily with mussels.

Symbiosis and commensalism exist in such communities. A few supposed instances affecting mussels are afforded by small forms that live within the shells in the mantle cavity of the mussel where they receive food and protection. A small bristle worm, *Chætogaster limnæi*, frequently observed in the mantle cavity of mussels, is supposed by some to be merely a commensal, but it may be considered a predacious species since it has been seen with juvenile mussels within its digestive tract (Howard, paper read at meeting of American Fisheries Society, 1918). The leech, *Placobdella montifera*, enters living mussels, but is not known to feed upon them (Moore, 1912, p. 89).

Bryozoa and other sessile forms are found attached to the exposed portions of live-mussel shells. Doubtless there are many cases of commensalism to be revealed by closer study of mussels in their natural habitat.

An interesting symbiotic relation exists between a mussel and the bitterling, a small European fish, which lays eggs in the mantle cavity of a fresh-water mussel which in turn infects the fish with glochidia (Olt, 1893). A different relation, which shows some reciprocity, however, is that of the fresh-water drum (*Aplodinotus grunniens*) of the Mississippi Basin, that eats fresh-water mussels but pays for the privilege, in part at least, by nourishing the young of several species parasitically encysted on its gills. (Surber, 1913, p. 105, and Howard, 1914, pp. 37 and 40.) The same is true of other fish that eat mussels, as the catfishes.

Parasitism is a phenomenon of community relations, and it is of double significance in the case of mussels, because not only have the mussels parasites to prey upon them, but they with few exceptions depend for existence upon the opportunity to become parasites of fish or, in one case, of an amphibian. A rather close relationship of fish to the mussel community is essential, and there may be a particular interrelation of given species of fish and of mussels. Questions arise as to when and how this special and intimate relationship came about and to what extent the habits of host and mussel interlock in such cases as the gar pikes and the sand-shells (Howard, 1914a), the river herring and the niggerhead, the shovel-nose sturgeon and the hickory-nut, the catfiches and the warty-back, the mud puppy and the little salamander mussel. In the last-named case, the peculiar habit of the mussel which lives beneath flat stones conforms evidently to the habits of the host, for the mud puppy is well known to frequent such situations.

One feature of certain mussels that possibly serves to decoy fish is the elaborate development of the mantle flap in gravid females of the pocketbook mussel, *Lampsilis ventricosa*, and others. (See p. 85.) These flaps in their form and coloration, including an eyespot, resemble a small fish, and the motion of these in the current still further enhances the resemblance. The enlarged marsupia distended with glochidia lie close to these flaps, one on each side. It has been suggested that a fish darting at this tempting bait may cause the extrusion of the glochidia and then become infected. (See Wilson and Clark, 1912, pp. 13, 14.) The unwelcome members in the associations to which mussels belong are discussed in the following section on "Parasites and Enemies."

PARASITES AND ENEMIES.

PARASITES.

Long green algæ are occasionally found attached to the exposed tips of the shells of mussels, and these may cause some erosion of the shells. Marly concretions, composed of intermingled low algæ and lime often form knoblike lumps on shells in lakes.

Among the most common of mussel parasites are water mites which dwell in the gill cavity and lay their eggs within the flesh of the mussel, in the inner surface of the mantle, in the foot, or in the gills. These water mites, which belong to the genus Atax, vary in size and color and to some extent in shape (Wolcott, 1899). One is black with a white Y-like marking on its back; others may be reddish. The largest and most degenerate is of a honey color with white treelike markings, but because of its inconspicuous coloration it is often overlooked. The different species of Atax are hard to distinguish without special preparation and study. Under magnification these water mites look somewhat like spiders. Small pearls are sometimes formed about Atax eggs.

Leeches are occasionally seen on the inner surface of the mantle of some mussels, especially in Anodontas (floaters) in ponds. They probably feed on the mucus of the mussel.

A small organism closely resembling a minute leech in general shape and appearance is occasional in the axils of the gills of mussels in some lakes. This is *Cotylaspis insignis*, one of the trematodes or flukes (Leidy, 1904, p. 110). One mussel may harbor a dozen or more of these parasites. Rather similar to *Cotylaspis insignis* but considerably larger and pink instead of yellowish, is the trematode *Aspidogaster conchicola*. It is more complex than *Cotylaspis insignis* and is usually found in the pericardial cavity of the host mussels, although in severe infection it may overflow into other organs.

Distomids, both free and encysted, are found in mussels. The distomid occurs in almost any muscular part of the body but most frequently in the foot or along the edges of the mantle. Sometimes pearls are formed around distomid cysts. The free distomids are usually found on the mantle surface next to the shell; they are chiefly confined to the flesh along the hinge line but may extend lower down. They are often associated with small irregular pearls. Sporocysts of distomids are common, especially in some Quadrulas. Many distomid parasites of mussels appear to be harmless, but one, *Bucephalus polymorphus*, destroys their reproductive organs (Kelly, 1899, p. 407; Wilson and Clark, 1912, pp. 69, 70; Lefevre and Curtis, 1912, p. 121). An ascarid worm is occasionally found in the intestine of mussels.

A worm with peculiar hooks on its head was found encysted in the margin of the mantle of some mussels in a pond near Fairport, Iowa. It was probably a trematode but has been found only once and never identified.

An oligochæte worm, *Chætogaster limnæi*, is occasionally found in mussels. It is possibly a parasite of snails from which it now and then migrates to mussels. We have some reason to believe that it devours the other mussel parasites. The crystalline style, a long translucent gelatinous body which is formed by the mussel within its intestine, is often mistaken by clammers for a worm.

Certain protozoa, *Conchopthirus curtus* and *Conchopthirus anodontæ*, somewhat resembling in general appearance the slipper animalcule, Paramœcium, are occasionally met in the mucus of mussels. Attached protozoa, like Vorticella, are also occasionally found on the edge of the mantle.

Occasionally larval Atax migrate into the space between the mantle and shell and are covered by nacre, where they may form minute white tracks, or in some cases apparently small raised "blisters" or pimples (Clark and Gillette, 1911). One or perhaps several species of distomid causes a brick-red or purplish discoloration of the nacre, mostly in thin-shelled mussels (Anodonta and Strophitus) (Osborn, 1898; Kelly, 1899, p. 406; Wilson and Clark, 1912, p. 66). The marginal cyst distomid sometimes causes a steel-blue stain of the nacre near the margin (Wilson and Clark, 1912, p. 63).

ENEMIES.

Mussels have numerous enemies, among which may be mentioned the mink, the muskrat, the raccoon, water birds, turtles, fishes, hogs, and man.

Of the depredation of many of these we know little. Water birds probably kill but few mussels, and of fishes, catfish and the sheepshead, or fresh-water drum, are the most noteworthy. These probably feed mainly on the thinner-shelled species. Small mussels (*Lampsilis parva*) have been found in the intestines of the turtle, *Malaclemmys lesueurii*.

Besides man the muskrat is the most notorious enemy of mussels, and the shell piles left by them are often conspicuous objects along the shores of lakes and rivers. Conchologists sometimes rely upon the muskrat's shell piles to furnish them choice and rare shells. Evermann and Clark (1918, p. 284) found not a few examples of *Micromya fabalis* in muskrat shell piles on the banks of Lake Maxinkuckee, though collecting in the lake during several seasons failed to reveal a single living specimen. Clammers prospecting new rivers sometimes use the piles of shells left by the muskrat as aids indicating where to dredge for shells.

Direct observations of the work of muskrats in Lake Maxinkuckee, Ind., were made by Clark and reported in "The Unionidæ of Lake Maxinkuckee" (Evermann and Clark, 1918, pp. 261, 262), as follows:

> The greatest enemy of the lake mussels is the muskrat, and its depredations are for the most part confined to the mussels near shore. The muskrat does not usually begin its mussel diet until rather late in autumn, when much of the succulent vegetation upon which it feeds has been cut down by the frost. Some autumns, however, they begin much earlier than others; a scarcity of vegetation or an abundance of old muskrats may have much to do with this. The rodent usually chooses for its feeding grounds some object projecting out above the water, such as a pier or the top of a fallen tree. Near or under such objects one occasionally finds large piles of shells. The muskrat apparently has no especial preference for one species of mussel above another but naturally subsists most freely on the most abundant species. These shell piles are excellent places to search for the rarer shells of the lake.
>
> In the winter after the lake is frozen, great cracks in the ice extend out from shore in various directions, and this enables the muskrat to extend his depredations some distance from shore in defi-

nite limited directions. During the winter of 1904 a muskrat was observed feeding on mussels along the broad ice crack that extended from the end of Long Point northeastward across the lake. The muskrat was about 50 feet from the shore. It repeatedly dived from the edge of the ice crack and reappeared with a mussel in its mouth. Upon reaching the surface with its catch it sat down on its haunches on the edge of the crack and, holding the mussel in its front feet, pried the valves apart with its teeth and scooped or licked out the contents of the shell. Some of the larger mussels were too strong for it to open, and a part of these were left lying on the ice. The bottom of the lake near Long Point, and also over by Norris's, is well paved by shells that have been killed by muskrats. Muskrats do not seem to relish the gills of gravid mussels; these parts are occasionally found untouched where the animal had been feeding.

In spite of all these enemies mussels held their own and throve and flourished until the appearance of man upon the scene, when depletion of the mussel beds became noticeable. Man exterminates a good many mussel beds by sewage discharge, by drainage, through which sand is washed down over the beds, by dredging and construction of wing dams for navigation, by pearling, but, most of all, by exhaustive clamming for the shells.

CONDITIONS UNFAVORABLE FOR MUSSELS.

Since mussels are animals of generally sedentary habit, with limited powers of locomotion, they are more helpless to escape from unfavorable conditions of environment than are fish or other active creatures of the water. This relative helplessness does not characterize the adult mussel alone, but is even exaggerated for the young stages. From the time the larval mussel attaches itself to a fish until it is liberated it is entirely dependent upon the movements of its host for its future home; it may be dropped in a suitable environment or in a place wholly unfavorable to its survival. On the other hand, adult mussels of many species can endure unfavorable conditions for a considerable period of time. This is found to be especially true of several species of Quadrula.

NATURAL CONDITIONS.

Some natural conditions unfavorable to mussel life are shifting bottom, turbidity, sedimentation, floods, and droughts. These conditions pertain usually to streams rather than to lakes. They have received some consideration in various paragraphs of this section on "Habitat"; therefore it is only necessary to summarize them in this connection.

The paucity of mussels in the Missouri River, as well as in the greater part of the Red River and other streams of the plains, is no doubt due to its exceedingly shifting bottom. Similar conditions apply in lesser degree in the lower stretches of many streams. In fact, all rivers, for some distances above their mouths, are as a rule very deficient in mussels as compared with sections farther up where bottom and other conditions are more favorable. Shifting bottoms not only prevent mussels from securing a foothold, but may also entirely destroy established beds.

Interrelated with shifting bottom are turbidity and sedimentation. All three factors and the extent to which they may be operative are largely dependent upon flood conditions. In nearly all large rivers floods commonly plow new channels here and there in the stream bed, cut away banks to a greater or less extent, and build new shoals or change the form and dimensions of old ones. Such changes in navigable streams are familiar to pilots who find it necessary to ' learn the river" each season. Many of these changes must be catastrophic to mussels in certain localities.

Excessive turbidity with consequent increased sedimentation, when of considerable duration, is no doubt seriously unfavorable to the well-being of mussels. It has been stated that mussels do not feed during periods of high turbidity, but no definite data in support of this can be given. That mussels do not "bite" well on the crowfoot hooks during a rising stage of water is a condition recognized by clammers. Whether the fact that the shells are not generally open and the mussels feeding at this time is due to the turbidity, or to other changing conditions incidental to the rising water, can not be stated. If heavy deposits of sediment are unfavorable for adult mussels, they must be more directly harmful to the young during the early stages of independent life, for the tiny juveniles may be smothered by deposits that would have less disastrous effect upon larger mussels.

The effects of droughts are ordinarily felt but little by the mussels of the larger streams and lakes. The most unfavorable condition arises when, owing to a prolonged dry season, the water is lowered to such an extent that the mussels fall easy prey both to muskrats and to clammers and pearlers seeking them in the shallow water. Crows, too, are known to pluck out and kill Anodontas when the water over them becomes low and clear.

In the small streams, lakes, and sloughs, the mussels may be killed by the partial or complete drying up of the water. Certain species of mussels are, of course, more resistant to such condition than others. Isley (1914) states that live specimens of *Unio tetralasmus* were plowed up in a pond three months after it had become dry. The mussels had burrowed down to zones of moisture.

ARTIFICIAL CONDITIONS.

Among the conditions imposed by man that may be detrimental to mussel life in our streams may be mentioned the discharge of sewage, industrial wastes, dredging, and the building of wing dams. (See Pls. IX, X, and XI.)

Disposition of the sewage and wastes of large cities without harmful contamination of the rivers presents an issue of growing importance. Portions of streams just below important cities are sometimes veritable cesspools, unsuited to both mussel and fish life. The Illinois River for a considerable distance below its origin is greatly influenced by sewage pollution through the Des Plaines River and the drainage canal; from the head of the stream down to Starved Rock, 42 miles from the source, no mussels are found, and a normal variety and abundance of fishes is not present above Henry, 77 miles from its source (Forbes, 1913, p. 170; Forbes and Richardson, 1919, p. 148). Industrial wastes from pulp and paper mills, tanneries, gas plants, etc., are injurious to fishes, and no doubt harmful to mussels as well. Such unfavorable conditions as arise through the depletion of oxygen supply by the decomposition of sewage are partially or completely corrected by the intervention of rapids or waterfalls. (See Shelford, 1919, p. 111, and Baker, 1920.)

River improvement work, such as dredging and the building of wing dams, creates conditions more or less unfavorable for mussels. Hydraulic dredging may destroy mussels, either directly by pumping them up, or by shifting the river channel so that ensuing changes cause new sand bars to form and to bury previously existing beds. Wing dams constructed for improvement of the Mississippi River, built of rock and brush and projecting from the shore to the channel, have far-reaching effects upon the course of the current, upon sedimentation, and upon the formation of sand bars. The area between the dams may fill up with sand, so that eventually willows are growing where a mussel bed once flourished. Such changes have been observed in the Mississippi River near Fairport, Iowa, and at Homer, Minn.

The effect of the construction of dams directly across the channel of a river, as for water-power development, has been discussed on page 97.

Greater irregularity of stream flow resulting from the clearing of forests greatly influences the life of mussels. The drying up of ponds inhabited by mussels and the extreme low stages of water which allow clammers to obtain the mussels by wading, form disastrous conditions to which mussel beds are occasionally exposed. Extreme low stages of lakes and streams in summer may lead to mortality of mussels resulting from high temperature of the water and diminished oxygen supply. (See Strode, 1891; Sterki, 1892; Farrar, 1892.)

GROWTH AND FORMATION OF SHELL.

MEASUREMENTS OF GROWTH.

Methods of propagation, estimate of results, and measures for protection all depend in a considerable degree upon knowledge of the rate of growth of mussels. It is important to know how many years elapse before a mussel may attain a market size, as well as at what age it may be expected to begin breeding. Furthermore, these questions require answers for more than 40 economic species, even if consideration were not given to the more than 500 additional American species of fresh-water mussel. The rate of growth is not, however, easily ascertainable for most species.

Mussels of any species may be left under observation for a considerable period in tanks or troughs, but experiments indicate that normal growth does not occur under the conditions of life in tanks. Even large ponds do not offer the conditions required by many species. The data to be offered on this subject are derived principally from experiments conducted at the Fairport station. Further data on growth of mussels will be found in Isley's paper (1914).

Pocketbooks, *Lampsilis ventricosa*, reared in one of the ponds at the Fairport station attained a length of 41 to 47 mm. (1.6 to 1.85 inches) in two growing seasons, and about 65 mm. (2.56 inches) by August of the third season. Examples 45 to 47 mm. long (1.76 to 1.85 inches), and these evidently in the second year of free life, were measured and planted in the Mississippi River by Lefevre and Curtis in June, 1908, and recovered by the senior author of this paper in November, 1910, at the close of the fourth year of growth (Lefevre and Curtis, 1912, p. 180 ff). They had attained lengths of 81 to 85 mm. (3.18 to 3.35 inches). (See fig. 6, p. 133.)

It is evident, then, that pocketbook mussels under only ordinarily favorable conditions may attain a marketable size by the end of the fourth season of independent life (at 3½ years of age from date of infection). The observations reported in the following table (10) show that a nearly equal rate of growth applies to the Lake Pepin mucket, *Lampsilis luteola*.

TABLE 10.—AVERAGE LENGTH OF SIX EXAMPLES OF THE LAKE PEPIN MUCKET, LAMPSILIS LUTEOLA, REARED IN POND 3D AT FAIRPORT, IOWA.

Time of measurement.	Length.	
	Millimeters.	*Inches.*
Close of second growing season	43.4	1.71
Close of third growing season[a]	68.8	2.72
Close of fourth growing season	77.0	3.04
Close of fifth growing season	80.6	3.18
Close of sixth growing season	84.9	3.35

[a] The records of the original lot for the third year having been lost in the fire, there is substituted a corresponding record for the third year of mussels of another lot recorded in Pond 8D. The mussels in Pond 3D were from a fall infection and those in 8D from a spring infection; therefore the former are slightly older.

Another species of pocketbook, *Lampsilis* (*Proptera*) *capax*, had attained a length of 49 mm. (1.93 inches) at the end of the second season, indicating a slightly more rapid growth for this species than for *Lampsilis ventricosa*. Thinner-shelled species of the genus Lampsilis may grow more rapidly. Thus some examples of the paper-shell *Lampsilis* (*Proptera*) *lævissima*, known to be not over 16 months of age (in free life), had attained lengths of 78 to 81 mm. (over 3 inches). An example of the paper-shell, *Lampsilis* (*Paraptera*) *gracilis*, grew from 17.6 mm. (0.7 inch) to 107 mm. (4.2 inches) in 2 years 9 months and 18 days, the rate of growth averaging about 1⅓ inches per year.

The very thin-shelled mussels of the genus Anodonta grow even more rapidly. Examples of the floater or slop-bucket, *Anodonta corpulenta*, taken from a pond at the Fairport station 16 months after the ponds were constructed, varied in length from 66 to 88 mm. (2.59 to 3.46 inches). Examples of another paper-shell, *Anodonta suborbiculata*, taken at the same time from another pond of the same age, but which may have offered less favorable conditions, were 64 to 67 mm. in length (2.52 to 2.63 inches).

With regard to heavy-shelled mussels, such as the niggerhead, pimple-back, and blue-point, there is much less satisfactory evidence as to growth. They undoubtedly grow much more slowly than mussels possessing thin shells, yet the rates of growth secured in such experiments as have been conducted can hardly be assumed to be representative of the conditions prevailing in nature. The species are not well adapted to life in tanks or ponds, and there are few places where measured specimens can be placed in rivers with any assurance that they will remain undisturbed or may be recovered at a later time. In Lefevre and Curtis's experiments (1912) an example of the hickory-nut, *Obovaria ellipsis*, that was practically full-grown when first measured, gained 5 mm. (one-fifth of an inch, 0.197) in a little less than 2½ years. In the same period an example of *Quadrula solida*, somewhat less mature, gained 10 mm. (two-fifths of an inch, 0.394).

In the following table (11) there are indicated sizes, at the close of the second year, of certain mussels reared accidentally or intentionally in ponds at the Fairport station. The short-term breeders, at least, were a little less than 1½ years of age.

Since these are all mussels of river habit, it can not be assumed that the growth attained in ponds is representative of the rate of growth in a natural environment.

TABLE 11.—SIZES AT CLOSE OF SECOND YEAR OF CERTAIN MUSSELS REARED IN PONDS, FAIRPORT STATION, IOWA.

Scientific name.	Common name.	Length.	
		Millimeters.	*Inches.*
Lampsilis ligamentina	Mucket[a]	20.0	0.79
Lampsilis anodontoides	Yellow sand-shell[b]	41.0	1.62
Obliquaria reflexa	Three-horned warty-back	16.0	.63
Obovaria ellipsis	Hickory-nut	11.4	.45
Plagiola donaciformis		20.0	.79
Quadrula plicata	Blue-point	13.5	.53
Quadrula pustulosa	Pimple-back	24.2	.69
Quadrula undata	Pig-toe	15.8	.62

[a] Other observations indicate that the mucket grows more rapidly in streams.
[b] The yellow sand-shell was only 1 year and 3 months of age.

Some medium-sized examples of several species of Quadrula were placed, after measurement, in a crate which was anchored in the Mississippi River at Fairport, September 19, 1910. When the crate was recovered and the mussels remeasured, July 31 of the following year, very little growth was apparent in most of the specimens. The data for measurements of length in the several examples are given in the following table (12):

TABLE 12.—INCREASE IN LENGTH OF MUSSELS IN CAGE.

Scientific name.	Common name.	Length, Sept. 19, 1910.	Length, July 31, 1911.	Increase in length.
		Inches.	*Inches.*	*Inches.*
Quadrula ebenus	Niggerhead	1.92	1.98	0.06
Quadrula pustulosa	Pimple-back	1.74	1.85	.11
Quadrula metanevra	Monkey-face	1.70	1.86	.16
Quadrula plicata	Blue-point	2.80	3.02	.22
Quadrula undata	Pig-toe	1.41	1.74	.33

In another experiment 76 mussels, representing 19 species, principally the thick-shelled forms, were placed in a crate with nine compartments which was anchored in the river about 25 feet from shore. The crate was put out July 31, 1911, and recovered November 14, 1913, when 36 of the original mussels, representing 13 species, were found to be alive. These mussels generally manifested a higher rate of growth than marked some of the mussels used in the experiment just described, although the increase in size was disappointingly small. The period of time between the dates of measurements was 2 years 3 months and 14 days. The mussels were of medium size at the beginning of the experiment, so that the growth to be expected was that which would characterize the period of approaching maturity rather than that of early life. The mussels living at the close of the experiment, with the maximum and minimum gain in length and the average for the species (when more than two examples were available), are shown in the following table (13):

TABLE 13.—GROWTH OF 36 MUSSELS IN CRATE FROM JULY 31, 1911, TO NOV. 14, 1913.

Scientific name.	Common name.	Examples.	Increase in length.		
			Maximum.	Minimum.	Average.
		Number.	*Inches.*	*Inches.*	*Inches.*
Quadrula ebenus	Niggerhead	7	0.64	0.38	0.463
Quadrula pustulosa	Pimple-back	5	.50	.20	.376
Quadrula pustulata	do.	1	.22		
Quadrula metanevra	Monkey-face	2	.46	.12	
Quadrula plicata	Blue-point	7	.80	.32	.517
Quadrula undata	Pig-toe	2	.49	.38	
Obovaria ellipsis	Hickory-nut	4	.72	.20	.455
Obliquaria reflexa	Three-horned warty-back	1	.18		
Tritogonia tuberculata	Buckhorn	1	.36		
Lampsilis ligamentina	Mucket	2	.84	.10	
Lampsilis recta	Black sand-shell	1	1.76		
Strophitus edentulus	Squaw-foot	2	.66	.56	
Unio gibbosus	Spike	1	.17		

It must be borne in mind that the conditions of life for mussels in an inclosed crate, and relatively closely crowded together, are probably not nearly so favorable for growth for the majority of mussels as are those of the natural river bottom, where the mussel has a fair chance to assume its desired position and secures the full benefit of the food-laden current. Doubtless the maximum rate of growth shown in the crate is more nearly normal than the average rate. Our impression is that thick-shelled mussels, such as the niggerheads, pig-toes, and pimple-backs, after they are half grown, increase in size ordinarily at the rate of a quarter of an inch a year or less. If this be true, it would require four years or more for a niggerhead mussel, under ordinarily favorable conditions, to increase from a length of 2 inches to a length of 3 inches. Assuming that the rate of growth is more rapid in early life, it may be inferred that niggerheads or pimple-backs 3 inches in length are 10 or 12 years of age. Additional experiments conducted under proper conditions are clearly wanted.

A marked contrast in rate of growth is thus afforded by the species of Quadrula (and others having generally similar character of shell), on the one hand, and those of Lampsilis, on the other. This was strikingly shown, in connection with the last experiment described, by two examples of the yellow sand-shell, *Lampsilis anodontoides*, which were not put into the crate but which must have found their way in by chance when still small enough to pass through the screen wire of ½-inch mesh. Although the crate was out only a little over two years, these two sand-shells were respectively 3.30 and 4.12 inches in length. Being elongate in form, they may have entered the crate when a little more than an inch in length.

Table 14 embodies the result of measurements of length and counts of rings on yellow sand-shells, *Lampsilis anodontoides*, from the St. Francis River, at Madison, Ark.

TABLE 14.—CLASSIFICATION OF 40 YELLOW SAND-SHELLS FROM ST. FRANCIS RIVER, ARK., ACCORDING TO LENGTH AND AGE.

Length in inches.	Number each length.	Age as indicated by interruption rings on surface of shell.				
		Three years.	Four years.	Five years.	Six years.	Older.
3	1		[a]1			
3⅛	1	1				
3¼	1		[a]1			
3½	2		2			
3¾	4	2	2			
4	8	1	6	1		
4¼	6		5	1		
4½	3		3			
4¾	9		2	5	1	1
5	5			1	2	2
Total	40	4	22	8	3	3

[a] Shell with stunted appearance.

The observations indicate that mussels of this species in the St. Francis River attain a length of 4 to 4½ inches in 4 years, that they may attain a length of 4 inches in 3 years, and that 6 years or more are ordinarily required to attain a length of 5 inches.

In summary, the rate of increase in length of fresh-water mussels varies from 1½ or 2 inches per year for paper-shells (as *Lampsilis lævissima*) to ¼ inch (a little more or a little less) per year for the niggerhead and related species, while an intermediate rate of ¾ or 1✓ inch per year characterizes the muckets and pocketbooks, and a slightly more rapid rate the sand-shells. In general the rate of growth is so directly proportioned (in inverse ratio) to the thickness of shell of the species as strongly to suggest that the limiting factor of growth ordinarily is not organic food, but the mineral content of the water (p. 87).

PRESENCE OF SO-CALLED GROWTH RINGS.

The ages of animals may not infrequently be determined, at least approximately, by the "rings of growth," on teeth, scales, scutes, or otoliths (ear stones), or other hard parts of the body. A similar criterion of age determination is of course commonly applied to trees. More recently the rings on the scutes of terrapin and those on the scales and otoliths of fish have been used for the same purpose.

This method of determining age is generally based upon the belief that the cessation or the slowing down of growth during the winter season may cause the formation of a distinguishable line or band on a concentrically growing structure. By counting the number of winter lines or bands the number of winters through which the animal has passed is ascertained, or by counting the number of zones between such rings, beginning with the center zone, the number of seasons of growth is discovered. It is one thing to know that such rings are formed in winter, but quite another thing to learn just how or why the rings are formed. It is also of primary importance to determine whether or not similar rings may be formed upon any other occasion than the occurrence of a season of winter. In the case of the fresh-water mussel shell, at least, these questions can be answered by observations and experiments. (Coker, unpublished notes.)

Some years ago when collecting mussels in lakes in southern Michigan it was observed that the shells of the fat muckets were all marked with several conspicuous rings which were approximately equally spaced on all the mussels of a bed. It seemed a natural inference that these dark rings represented winter periods and thus afforded a means of age determination. At another time, upon examination of mussels which had been measured and placed in crates in the river two years previously, it was observed that there were rings apparently corresponding to the two winters which had elapsed since the date of original measurement, but that there was also another ring which marked the exact size of the mussel when originally measured. (See text fig. 6.) Subsequent observations showed that whenever a mussel was measured and replaced in the water, a ring would be formed on the shell before growth in size was resumed.

These observations led to an effort by microscopic examination of sections of the shell to determine the significance of rings which apparently could be formed either by a season of cold weather or by the procedure of taking a mussel from the water, applying a caliper rule, and returning it to the water. To make clear what was learned from the study of the sections it is necessary first to explain briefly the mode of formation of shell which leads to growth in size.

MODE OF FORMATION OF SHELL.

The shell is composed of four distinct layers (text figs. 1, 2, and 3). The outer is the horny covering called the periostracum.[a] Immediately beneath this is a calcareous layer composed of prisms of calcium carbonate set vertically to the surface. This prismatic layer is very thin, though thicker than the periostracum, and is likely to remain attached to the periostracum when that is peeled off. Beneath the prismatic layer and composing nearly the entire body of the shell is the nacreous or mother-of-pearl layer, which is made up of almost innumerable thin laminæ lying one upon the other and parallel to the inner surface of the shell. Through the nacre, intersecting its laminæ, passes a very thin fourth layer, the hypostracum,[a] secreted by the muscles (p. 172).

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[a] The fact that the periostracum itself comprises 2 layers of separate origin, while very significant in some respects, is immaterial in this connection.

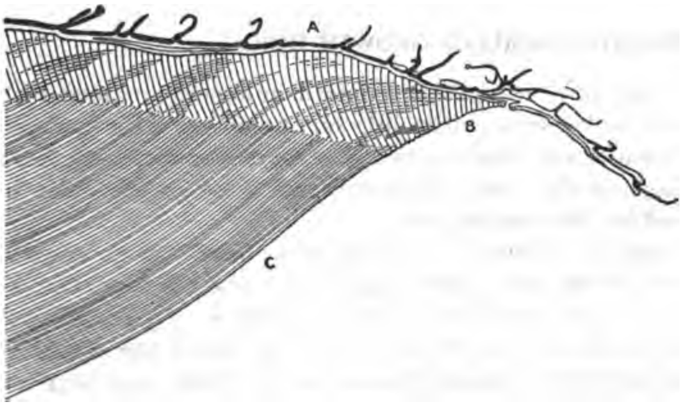

FIG. 1.—Diagrammatic and highly magnified camera lucida drawing of section of margin of fresh-water mussel shell, *Obovaria ellipsis* (Lea), showing arrangement of layers: *A*, epidermis (double layer); *B*, prismatic layer; and *C*, nacreous layer. Note the folds of epidermis which give the shell its "silky" appearance.

Growth of shell in thickness is accomplished by the laying down of successive laminæ, from the entire surface of the mantle. Layer after layer is added to the inner surface of the shell, each layer exceedingly thin and generally a little larger than the preceding. Ring after ring is added to the margin of the shell, but since growth is most pronounced in the posterior (rear) direction, less so in a ventral, and still less in the anterior (forward) direction the rings must be widest behind and narrowest in front. It will be noted that any mussel shell is marked with innumerable concentric lines. Superficially such lines suggest the annual rings seen on the section of the trunk of a tree, but the resemblance is entirely misleading. The shell is added to in layers, but a very great number of layers are made in a year. Pfund (1917) has, by refined physical methods, measured the thickness of the layers or laminæ and determined that the thickness in the examples he studied lies between 0.4 μ and 0.6 μ. Translating these terms into ordinary language, there are some 50,000 layers to an inch of thickness. A shell one-quarter of an inch thick would have 12,500 laminæ; and if such a shell were 8 years old, more than 1,500 laminæ would have been formed each year, on the average. The outcropping edges of these laminæ on the surface of a polished niggerhead shell have also been measured and found to be spaced at the rate of about 9,000 to the inch. Such lines are of course not visible to the naked eye, and therefore the fine rings in evidence on the surface of the shell can not represent these

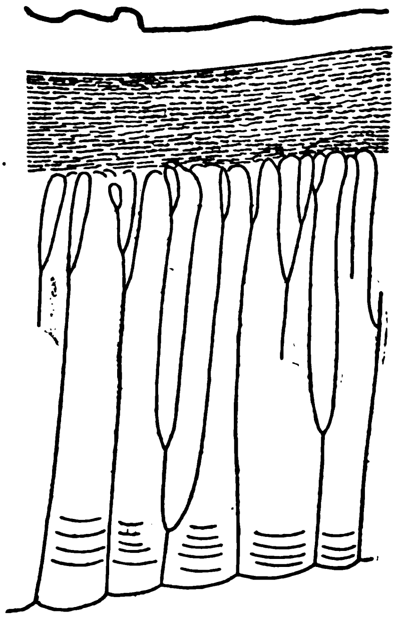

FIG. 2.—Section through double-layered periostracum and prismatic layer. Nacreous layer below not shown.

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[a] Not shown in figures herewith.

laminæ but must have some other significance. They probably mean nothing more than slight and frequent but irregular retractions of the margin of the mantle during the process of shell formation, which have registered themselves in fine wrinkles on the surface of the shell as it is built. The more conspicuous rings that mark some shells still await our attention.

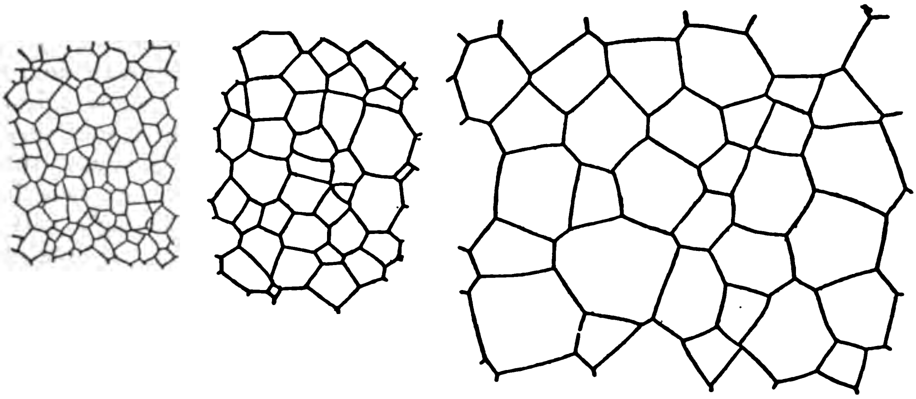

FIG. 3.—Sections through prismatic layer of *Quadrula ebenus*. The sections were made at different levels, the prisms being smaller and more numerous in the outer portion. × 300.

Growth of the shell in length and breadth is accomplished by the secretion of shell substance of the three layers by cells at or near the margin of the mantle. There are certain cells of a furrow in the margin of the mantle which form only periostracum, and there is a certain portion of the mantle near the margin which forms only prismatic shell substance, while the greater portion of the mantle surface normally forms only nacre. Now, the important point for our present consideration is this: If, from any cause, the margin of the mantle is made to withdraw within the shell to such an extent as to break its continuity with the thin and flexible margin of the shell, then, as the study of sections indicates, when the deposition of shell is resumed, the new layers of prismatic substance and periostracum are not continuous with the old, end to end, but are more or less overlapped by the old. In other words, growth does not begin again exactly where it left off, but a little distance back therefrom, and the cause of this is largely mechanical (text fig. 4). The amount of overlapping probably depends upon the degree of disturbance and the extent to which the mantle has withdrawn itself. The result is an unwonted duplication of layers. Counting inward from the

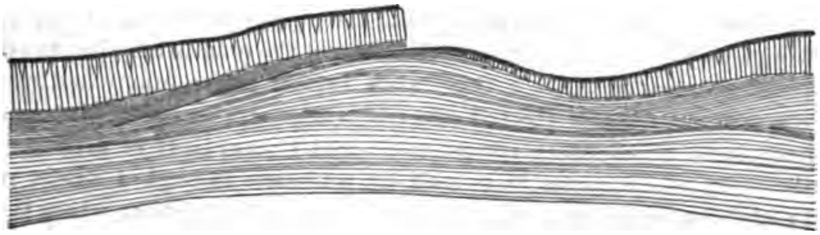

FIG. 4.—Section through the interruption ring on pocketbook mussel, caused by handling mussel in summer. Simple duplication.

outer surface we find not simply one series of periostracum, prismatic, and nacreous layers, but periostracum and prismatic layers, then periostracum and prismatic again, and finally the nacreous layer; the outer layers are doubled up.

SIGNIFICANCE OF RINGS.

In a case such as has just been described, where the outer layers are doubled up as a result of an extreme retraction of the mantle, the effect of seeing a second horny layer through the outer periostracum and the fairly translucent prismatic layer gives the appearance of a dark band on the shell. This is the so-called growth ring, which would be better termed duplication ring or interruption ring,[a] since its significance is simply that the continuity of the outer layers is interrupted and the break is repaired by overlapping. In other words, the periostracum and prismatic layers are "spliced" at this point. A duplication of layers should easily be observable on shells having fairly light-colored or translucent periostracum but not on shells having a very dark or opaque covering, and this is found to be the case. Growth rings or interruption rings are commonly seen on pocketbooks, fat muckets, yellow sand-shells, floaters, and other shells of light or only medium dark colors, while they are distinguishable with difficulty, if at all, on niggerheads, pimple-backs, blue-points, and other dark-colored shells.

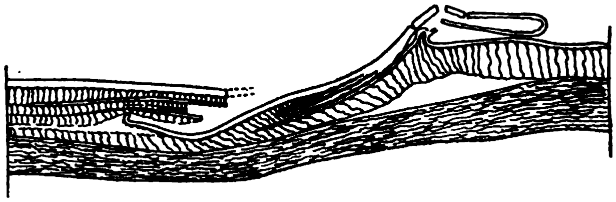

FIG. 5.—Section through interruption ring (winter ring) on shell of pocketbook, *Lampsilis ventricosa*, showing repeated duplications of periostracum and prismatic layers.

If the winter rings are formed in the same way, and the breaking of the continuity of the outer layers is due to the withdrawal of the mantle in cold weather, then it would be expected that several duplications would occur for a single winter. For cold weather does not ordinarily fall with one blow. Periods of cold and warm weather alternate for a time before winter sets fairly in, and again in the spring periods of low and high temperature alternate before winter is entirely passed. Such fluctuations of temperature are, of course, not so frequent or noticeable in the water as in the air, but they do occur. It might be expected that the mussel would react to the first sharp touch of winter by closure and a sharp withdrawal of the mantle but that the deposition of shell would be resumed after a time, while further interruptions and resumptions of growth would occur before the full effect of winter was experienced. Again in the spring there might be alternate interruptions and resumptions of growth. This, at least, is the story which seems to be told by a section through a winter ring when examined under the microscope. Text figure 5 shows such a section, where the alternation of periostracum and prismatic layers is repeated seven times, indicating six interruptions of growth. As virtually no increase in size occurs between the several interruptions, the duplicated or repeated layers are simply piled upon one another.

Interruption rings corresponding to seasons of winter differ from those corresponding to a single severe disturbance of the mussel during the normal period of growth in that the latter are rings of single duplication (text fig. 4), while the former show several repetitions (text fig. 5). The winter rings in shells that have been observed are, therefore, darker, though they may or may not be broader (text fig. 6).

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[a] See Isely, 1914, p. 18.

ABNORMALITIES IN GROWTH OF SHELL.

Seriously malformed mussels are not infrequently found, and peculiar interest attaches to these because shellers generally entertain the belief that a mussel with deformed shell is most likely to contain a pearl. It seems possible that this belief is not without some foundation. Pearls probably occur more frequently in parasitized mussels, and many of the observed malformations are undoubtedly due to parasites.

A few distomids upon the mantle of Anodontas along or near the dorsal fold evidently cause rusty stains in the nacre, abnormal growths on the inner surface of the shell, deformities of the hinge teeth, and dark or poorly formed pearls. Another parasite which infests the reproductive organs may almost completely destroy the gonads of the female mussel, and in such case the female may develop a shell in the form of a male or in a form intermediate between that of the male and the female. There is evidence that parasites found encysted in the margin of the mantle may give rise to stains on the nacre at the margin of the shell, that others cause the not unfamiliar steely or leaden-colored margins of shells, while some produce a pitting of the inner surface of the shell.

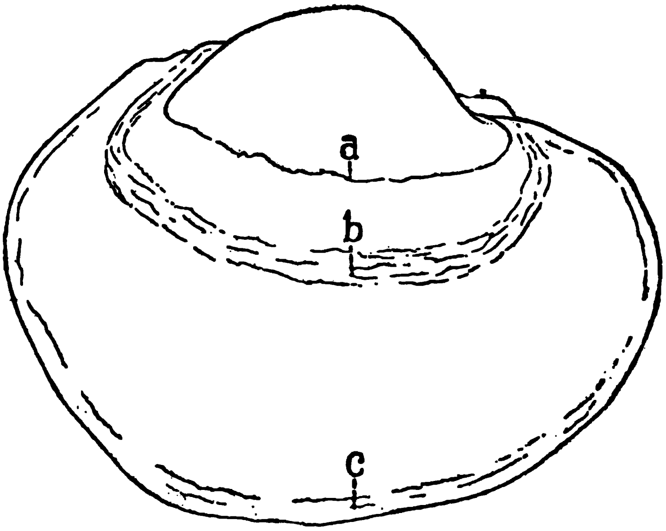
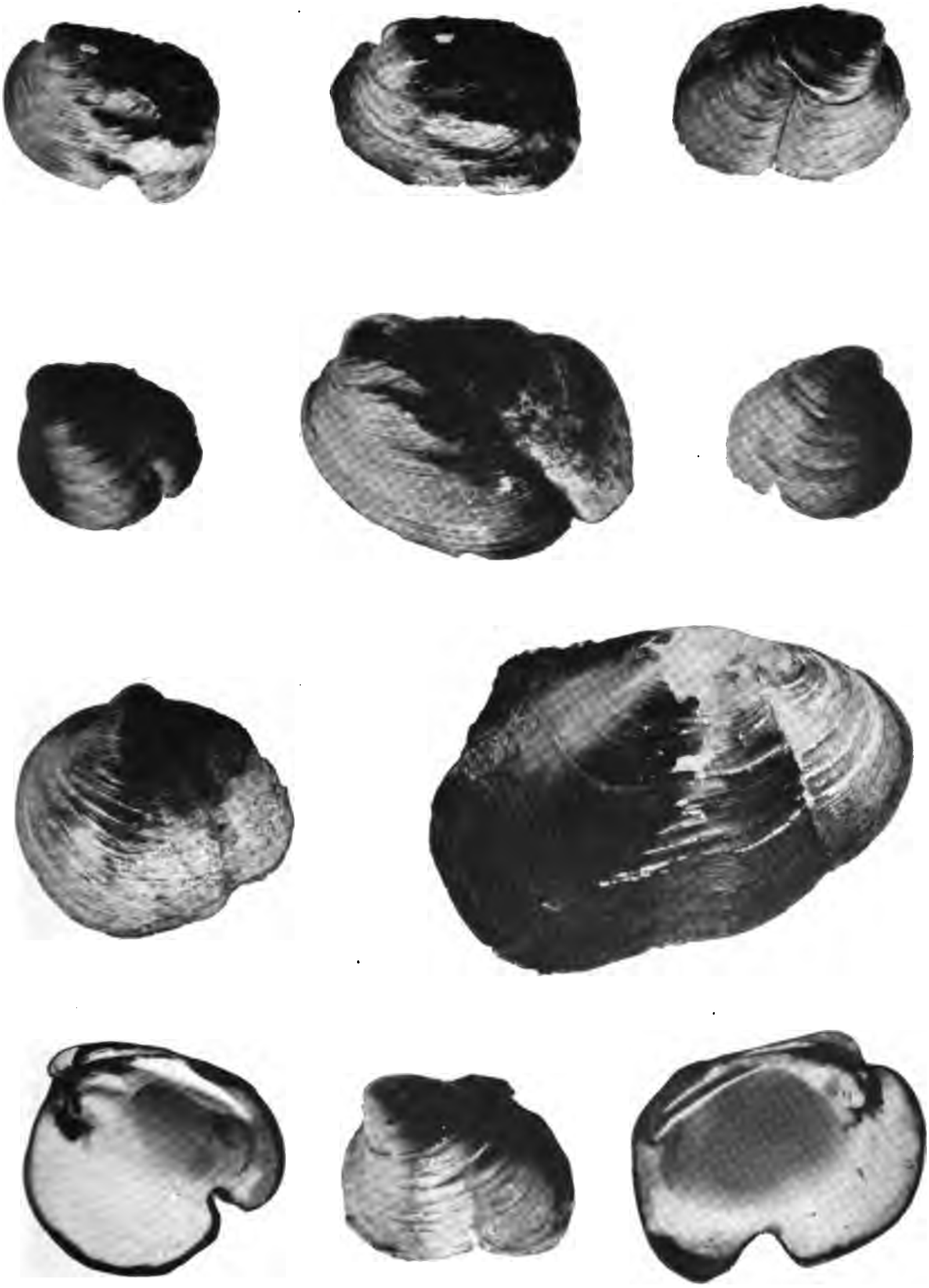


FIG. 6.—A shell of the pocketbook, *Lampsilis ventricosa*, which was recovered after having been measured and confined in a wire cage in the Mississippi River for two years, four and a half months. The line *a*, an interruption ring, marks the size at the time of measuring. The lines *b* and *c* evidently correspond to the two periods of winter intervening. The inconspicuous sign of a winter interruption preceding the date of measurement does not appear in the drawing. Natural size. (After Lefevre and Curtis.)

One of the most common and serious defects of otherwise valuable commercial shells is the presence of yellow and brown spots or bluish or greenish splotches in the nacre. Regardless of the texture of the shell, the partially or wholly discolored buttons must be given a very low grade. The spots are not always found upon the surface but may lie deep within the nacre, to be brought out in the finished button by the processes of shaping and polishing. Spotted shells are most common in certain rivers or parts of rivers, particularly where the current is sluggish as in partly inclosed sloughs. Some of these discolorations are often observed to be associated with a parasitized condition of the mussels, but it is not probable that the spots are always due to parasites. The U. S. Bureau of Standards, in connection with an investigation of the bleaching of discolored shells, has found that the dark-yellow and brown spots are mud fixed by the nitrogenous organic layer which binds together the calcium carbonate, and that the pale-yellow color is apparently due to an organic coloring matter in the organic layers. That bureau also reports that the color of the pink shells is due to an organic coloring which is not confined to the organic layer but permeates the whole shell.

A striking form of shell associated with the presence of parasites is that with abbreviated gaping anterior margins, the edges being much thickened and in appearance rolled outward. The explanation appears to be simply that the parasites check the peripheral growth of the forward portion of the mantle, or perhaps, as the result of irritation, keep the mantle more or less retracted in this portion. The shell being controlled in growth by that of the mantle, its forward extension is checked, while growth in thickness continues. Meantime the valves of the shell, growing normally in other directions, are gradually and naturally pushed apart as successive layers are added in the posterior portions. In consequence, after a time the valves of the shell cease to meet anteriorly when the posterior margins are apposed. The result is a shell of normal dimensions behind and below but abbreviated in front, where the edges are disproportionately thick and gaping.

A very familiar form of abnormality is shown by the shells in Plate XII. When a single shell of this type is first seen one is inclined to suppose that the deformity is the result of a mechanical injury; but when shells marked by almost identically the same abnormality are repeatedly found in various places and in different kinds of bottom, it becomes evident that the explanation of mechanical injury is not applicable. It is probable that a parasite checked the growth of the mantle at a particular point, so that, while growth of shell continued normally both before and behind, it was so retarded at that point that a permanently notched outline resulted. The subject of discolored and malformed shells is not introduced, however, with the object of definitely explaining them, but rather with a view to directing attention to the desirability of further investigations of the parasites of mussels, as well as of certain features of the environment of mussels, as regards their effects upon the form and quality of shells.



Illustrating a peculiar abnormality of not infrequent occurrence among fresh-water mussels.

[See text, page 139, and compare Plate XXI, fig. 1, showing marsupium occupying outer gills only. Figures after Lefevre and Curtis.]

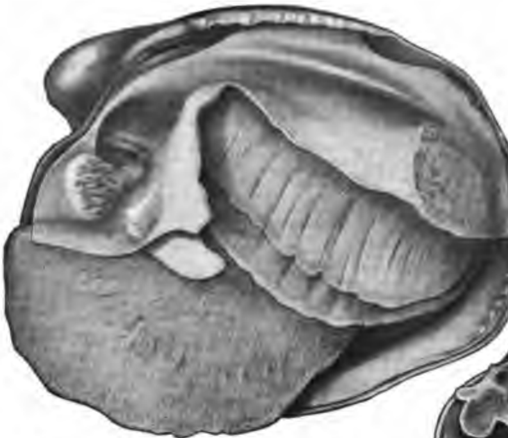


FIG. 1.—Niggerhead mussel, *Quadrula ebenus;* marsupium occupying all four gills.

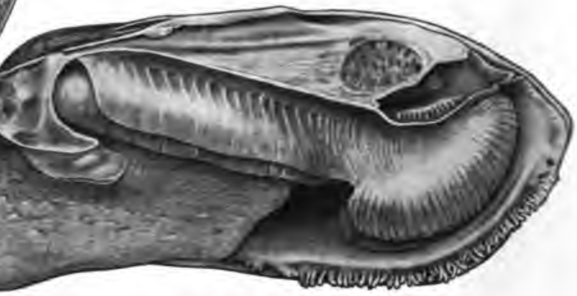


FIG. 2.—Black sand-shell, *Lampsilis recta;* marsupium occupying only posterior end of outer gills.

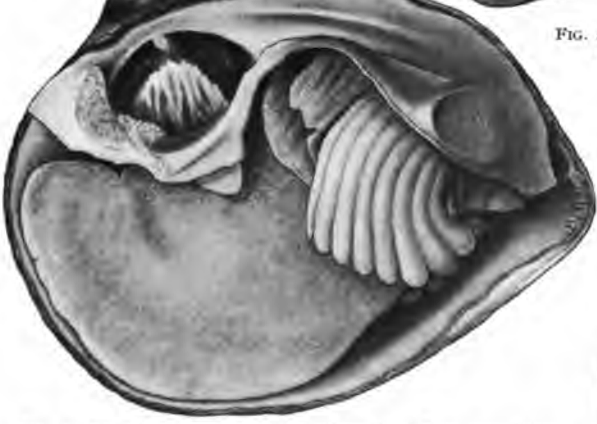


FIG. 3.—Three-horned warty-back, *Obliquaria reflexa;* marsupium occupying middle region of outer gills.

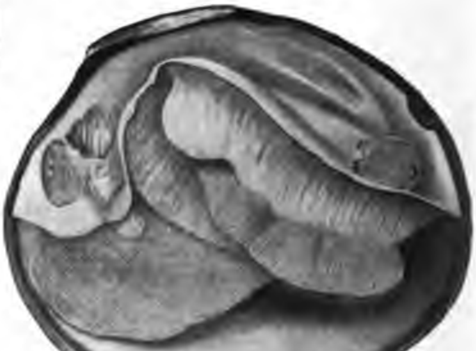


FIG. 4.—Dromedary mussel, *Dromus dromas;* marsupium occupying only lower border of outer gills. Anterior end of gill not included in marsupium but overhangs it.

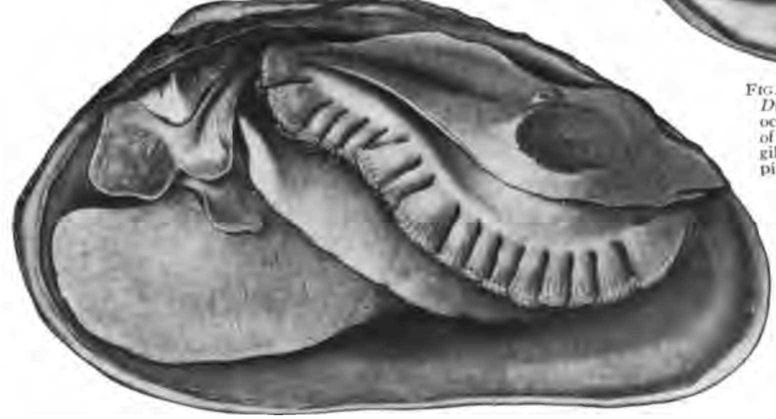


FIG. 5.—Kidney-shell, *Ptychobranchus phaseolus;* marsupium occupying entire lower border of outer gills and much folded.

PART 2. LIFE HISTORY AND PROPAGATION OF FRESH-WATER MUSSELS.

INTRODUCTION.

The life histories of fresh-water mussels present features in striking contrast to those of other familiar mollusks of our seas and rivers. The American oyster, the clam, the quahaug, and the sea mussel cast the eggs out to undergo development while floating in the water. The pearly mussels of rivers and lakes, on the contrary, deposit their eggs in marsupial pouches which are really modified portions of the gills, and there they are retained until an advanced stage of development is attained. This particular feature of breeding habit is not, however, unique to mussels. There are clams in coastal waters that incubate the eggs in the gills, and the common oyster of Europe displays a similar habit; but with all these the larvæ when released are prepared for independent life. Such is not the case with fresh-water mussels. When the larval mussels are discharged from the marsupial pouches, the mother has done all that she can for them; but they still want the services of a nurse or foster parent, as it were. Lacking the structure and appearance of young mussels, they display a peculiar form designated as glochidium, and (with few exceptions) they will not continue to live unless they become attached to some fish, upon which for a certain time they will remain in a condition of parasitism.

During the period of parasitic life the glochidium undergoes a change of internal reorganization, or metamorphosis, with or without growing in size. After the change is complete and a form somewhat similar to the adult is attained, the young mussel leaves the fish to enter upon its independent existence. At this time, or soon thereafter, some mussels, but not a great number, differ distinctly from the adult form in bearing a long, adhesive, and elastic thread, or byssus, by which they attach to plants, rocks, or other anchorage.

The life history, then, comprises the following five stages: (1) The fertilized and developing egg retained in the marsupial pouches of the mother mussel; (2) the glochidium, which, before liberation, is often retained for a considerable further period in the gills; (3) the stage of parasitism on fish (or water dogs); (4) the juvenile stage, which may or may not be marked by the possession of threads for attachment to foreign objects; and (5) the mussel stage, with the usual periods of adolescence and maturity.

Such in brief is the typical story of the life of a pearly mussel. And yet each species of mussel, and there are many, has its own characteristic story, which differs in more or less important respects from those of other species. One kind of mussel will pass through the stage of parasitism only upon a particular species of fish, while another kind acquires the aid of certain other fish. The diversity in life histories also manifests itself in such details as in the season of spawning, in the part of the gills in which the glochidia are carried, in the duration of the incubation period, in the matter of growth in size during parasitism, and in many other particulars. There are even some mussels which, like exceptions that prove the rule, undergo complete development without being parasites upon fish at any stage. It is advisable, therefore, to treat the several stages of life history at greater length and with such detail as is necessary to establish an understanding of the conditions necessary for the successful propagation of the various useful mussels and for the effective conservation of the mussel resources.

HISTORICAL NOTE.

It seems appropriate to remark that the considerable fund of knowledge which has been gained in very recent years regarding the diversified life histories of fresh-water mussels has been gained very largely as a result of scientific studies which have been stimulated by the practical need of conserving an economic resource, and which have been pursued preliminary to or in connection with the propagation of mussels as a measure of conservation. To put it in another way, the development of the fresh-water pearl-button industry has furnished an effective stimulus to biological studies of high scientific interest and importance, just as the application of science to studies of commercial mussels has rendered a distinct economic service.

As early as 1695 at least, the glochidium (see text fig. 8, p. 143) was observed in the gills of European mussels, and was understood to be the larval form of the mussel, although it was not then called a glochidium. Of the further stages of life history, science, as well as the public, remained in ignorance for a long time. So wide indeed was the gap of knowledge that it became possible for a scientific writer in 1797 to advance the theory that the little mollusks noted in the gill pouches were not young mussels, but were parasites of mussels constituting a genus and species of their own, which the investigator designated with the Latin name *Glochidium parasiticum*. This view, known as the Glochidium theory, though it never won full acceptance, was strongly supported, and an exhaustive inquiry and report upon the subject by a special committee of the Academy of Sciences in Paris, completed in 1828, failed to effect its decisive defeat. When, however, in 1832, Carus was fortunate in observing the passage of the eggs from the ovary of the mussel into the gill pouches, the false theory was definitely overthrown. The name glochidium, suggested though it was by an erroneous assumption, has persisted ever since, being now correctly understood to designate not a distinct animal but a typical stage in the development of the mussels.

It still remained to determine how and where this peculiar larva became transformed into the familiar adult mussel, and this important gap was abridged by Leydig, in 1866, when the glochidium was discovered in parasitic condition upon the fin of a fish.

The advance in knowledge of the life history of fresh-water mussels made in the ensuing decades was slow and inconspicuous, and textbooks, both American and foreign, continued to reproduce accounts based upon the inadequate observations of the life histories of European mussels. A period of distinct progress came with the extensive and admirable investigations conducted by Lefevre and Curtis (1910, 1910a, and 1912) in association with the Bureau of Fisheries during the years 1905 to 1911. These investigations served to reveal not only some of the distinctive features of the breeding habits and life histories of the American mussels as contrasted with the European species but also the great diversity existing among the many American species, in breeding season, period of incubation, and form of glochidia. The results of the investigations aggregated a mass of original observation on various phases of the propagation and life history of fresh-water mussels. Other investigations, notably Ortmann's (1911, 1912, etc.), have contributed materially to knowledge of the breeding characters and habits and the development of mussels, while Simpson (1899, 1900, 1914, etc.), Walker (1913, 1918, etc.), Ortmann (1911, 1912, 1913, etc.), and others have greatly extended our information regarding classification, distribution, and structure.

With the establishment of the Fisheries Biological Station at Fairport, Iowa, and the beginning of its scientific work in 1908, the studies pursued by the scientific staff of that station, in connection with the propagation of mussels, made still further advances. Chief among the results of the studies conducted at this station may be mentioned the discovery that particular species of mussels are restricted in parasitism to one or a few species of fish, the rearing of young mussels in quantity from artificial infections upon fish, the demonstration that the glochidia of certain species of mussels may grow materially in size during the period of life on the fish (being, therefore, true parasites), and the observation that one noncommercial species of fresh-water mussel normally completes its life history without a stage of parasitic life.[a]

Finally it should be remarked that one of the most difficult of all gaps to bridge was the rearing of young mussels after they leave the fish. Strange as it may seem, all attempts to keep alive and to rear the young mussels under conditions of control failed of result. Lefevre and Curtis (1912, pp. 182, 183) recorded the rearing from an artificial infection of a single young mussel which attained a size of 41 by 30 mm. In 1914, however, Howard was successful in rearing over 200 Lake Pepin muckets from an artificial infection, when the infected fish were retained in a small floating basket in the Mississippi River (Howard, 1915). These mussels attained a maximum size of 3.2 cm. in the first season; and in subsequent years many of them were reared to maturity, the glochidia developed from their eggs were infected upon fish, and a second generation was reared to an advanced stage. In that year (1914), too, Shira, using watch glasses and balanced aquaria, reared a few mussels from an artificial infection to a maximum size of 0.44 cm. in 291 days. In the same year, though from an experiment initiated by the senior author in the fall of 1913, young mussels were reared in a pond, from an artificial infection of fish liberated in the pond, to a maximum size in the first season of 3.5 cm. Some of these mussels at the age of 4 years had attained sizes suitable for commercial use in the manufacture of buttons. The same species, *Lampsilis luteola* (Lamarck), known as the Lake Pepin mucket, was used in all of these experiments. Subsequent experiments on a larger scale conducted both at Fairport and in Lake Pepin are mentioned on a later page.

AGE AT WHICH BREEDING BEGINS.

The age at which mussels begin to breed varies with the species. There is reason to believe that the paper-shell, *Lampsilis* (*Proptera*) *lævissima*, breeds in the same summer during which it leaves its host or when just 1 year of age from the egg. *Anodonta imbecillis* and *Plagiola donaciformis* apparently breed in the second summer. The smallest breeding Quadrula observed was a pig-toe, *Quadrula undata*, 30 mm. (about 1.2 inches) in length, and 4 or 5 years of age as evidenced by the interruption rings. The smallest washboard, *Quadrula heros*, observed in breeding condition was 91 mm. (3.58

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[a] Lefevre and Curtis (1911) had previously observed and reported the fully developed juvenile mussels in the gills of *Strophitus edentulus*. Later, Howard (1914) while showing that the glochidia of that species will become parasitic on fish and undergo development under the usual conditions, discovered that another species, *Anodonta imbecillis*, normally develops without the aid of fish. (See p. 156, below.)

inches) in length and of an estimated age of 8 years. Females of the Lake Pepin mucket, *Lampsilis luteola*, reared at the U. S. Fisheries Biological Station, Fairport, Iowa, were found with mature glochidia in the third season of growth, a period of slightly more than two years after dropping from the fish. Undoubtedly not all species breed at such an early age, and it perhaps takes the heavier Quadrulas 6 or 8 years to reach the breeding age.

OVULATION AND FERTILIZATION.

With a few exceptions,[a] the sexes are separate in American species of fresh-water mussels. The discharge of eggs (ovulation) has been observed in some instances (Latter, 1891; Ortmann, 1911, p. 298; and Howard, 1914, p. 35). The eggs pass from the ovaries by way of the oviduct, through the small genital aperture into the cloaca and suprabranchial chambers, and then into the portions of the gills which are to serve as brood pouches. The sperm which has been thrown out into the water by one or more male mussels, doubtless those in the near vicinity of the female, is taken in by the female with the respiratory current, but whether the eggs are fertilized while on the way to the brood pouches or after reaching them is unknown, since the process of fertilization in nature has never been observed. We have no clue either as to the nature of the stimulus which may excite ovulation or as to how it may be timed so as to take place when a supply of living sperm is available in the water for the fertilization of the eggs. Certain it is that the eggs are usually fertilized, although in the brood pouches of any gravid mussel that may be examined there are found a good many eggs that have failed to develop, presumably because they have escaped fertilization.

The discharge of sperm in great quantities may not infrequently be observed when male mussels are retained in aquaria. The writers have observed in a large tank at the Fairport station a male mussel discharging sperm. During the process it traveled extensively over the bottom, leaving in the sand a long winding furrow which was filled with a white cloud of sperm. Perhaps the discharge of sperm and its introduction with the respiratory current into the female constitute the exciting cause of ovulation. Experiments are clearly wanted to determine this question. The arrangement of the eggs in the several chambers of the brood pouches varies according to the character of the pouch, and will therefore be more conveniently described in the following section.

BROOD POUCHES OR MARSUPIA.

The gills of mussels, as of other lamellibranch mollusks, are thin flaps that hang like curtains from each side of the body, a pair on each side. As explained in another place (p. 175) each gill, thin as it may appear, is really a double structure, or more correctly is a sheet folded upon itself just as a map, larger than the page of a book in which it is bound, is folded on itself. There is this difference; the map may be unfolded at will, but the gill may not, because the two sections are attached together by many parallel partitions which divide the narrow space between the sheets into a lot of long slender tubes. It is into these tubes that the eggs are deposited, and when filled with eggs or glochidia the several tubes are greatly distended (text fig. 7). The entire gills or the parts of the gills bearing the eggs then appear not as thin sheets but as thick pads. In this condition the marsupial pouches might be compared to pods filled with closely packed beans, the individual beans representing not single eggs but separate masses of eggs.

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[a] The known exceptions are, occasionally, *Quadrula rubiginosa* and *pyramidata*, and *Lampsilis parva*, and, usually, *Anodonta imbecillis* and *henryana* (Sterki, 1898), and *Symphynota compressa* and *viridis* (Ortmann, 1911, p. 308).

When the tubes of a mature female mussel are empty the gills may be as flat as those of the males, or they may appear as sacks with thin translucent walls. The latter condition generally characterizes the long-term breeders, in which the portions of the gill intended to receive the eggs are permanently enlarged.

The marsupia are conspicuously colored in some species, but in different species the coloration is not necessarily attributable to the same cause. In the niggerhead, *Quadrula ebenus*, the pig-toe, *Quadrula undata*, and other species, the bright-red appearance of the marsupia is due to the deeply colored eggs showing through the thin walls of the marsupia. In the yellow sand-shell, *Lampsilis anodontoides*, the pocketbook, *Lampsilis ventricosa*, and the Lake Pepin mucket, *Lampsilis luteola*, the pigment lying in the outer walls of the ovisacs takes the form of dark bands on the lower portion of the marsupium, the pigmentation becoming more dense and conspicuous when the mussels are gravid. In the young *Lampsilis ellipsiformis* that we have seen the pigmentation is more intense and more general, extending even to the upper portion of the marsupia, but there restricted to the partitions separating the ovisacs. The color in the black sand-shell, *Lampsilis recta*, and the Missouri niggerhead, *Obovaria ellipsis*, is white or cream, in contrast to the yellowish color of the remainder of the ovisacs.

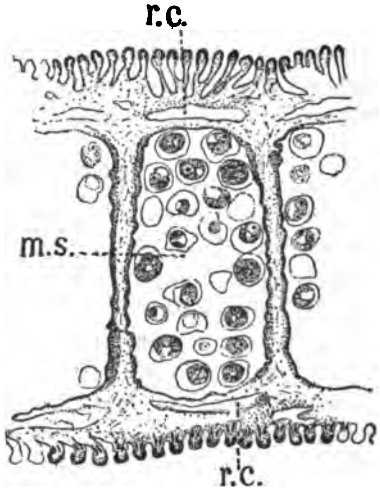

Fig. 7.—Horizontal section of a water tube of a gravid marsupium, showing respiratory canals (*r. c.*), and marsupial space (*m. s.*), containing glochidia. (After Lefevre and Curtis.)

The extent to which the gills are specialized or modified to receive and retain the eggs while they are developing into the glochidia has been largely utilized in the classification of mussels. All of the North American species belong to the groups in which the brood pouch or marsupium comprises either all four gills or only the outer gills. This group, in turn, is divided into the following seven divisions, according to the specializations involved (Simpson, 1900, p. 514):

1. Marsupium occupying all four gills, as in the niggerhead mussel, *Quadrula ebenus*, and perhaps all Quadrulas (Pl. XIII, fig. 1).
2. Marsupium occupying the entire outer gills, as in the heel-splitter, *Symphynota complanata* (Pl. XXI, fig. 1).
3. Marsupium occupying the entire outer gills, but differing from the second in that the egg masses lie transversely in the gills, as in the squaw-foot, *Strophitus edentulus*.
4. Marsupium occupying only the posterior end of the outer gills, as in the black sand-shell, *Lampsilis recta*, etc. (Pl. XIII, fig. 2).
5. Marsupium occupying a specialized portion in the middle region of the outer gills, as in the three-horned warty-back, *Obliquaria reflexa* (Pl. XIII, fig. 3).
6. Marsupium occupying the entire lower border of the outer gills in the form of peculiar folds, as in the kidney-shell, *Ptychobranchus phaseolus* (Pl. XIII, fig. 5).
7. Marsupium occupying the lower border only of the outer gills, but not folded, as in the dromedary mussel, *Dromus dromas* (Pl. XIII, fig. 4).

Most of the commercial species belong to the first and fourth types.

With such species as have all four gills, or the entire outer gills serving as marsupia, the sexes are scarcely, if at all, distinguishable from an examination of the shell; but when a distinct portion of the outer gill is used as a brood pouch there is usually a pronounced inflation of the shell over the region of the marsupia, so that the female mussel is clearly marked on the exterior. (See also Grier, 1920.)

It is to be remarked that the eggs packed into the water tubes or marsupial chambers do not usually remain free of each other, but become either attached together by their adhesive membranes or else embedded in a common mucilaginous substance. When the eggs or glochidia are removed from the gills they do not separate from one another unless fully ripe, but remain in large masses which conform to the shape of the tubes from which they have been removed[a] (Pl. XIV, figs. 8–11). It occurs frequently when gravid mussels are disturbed that the eggs, in whatever stage of development they may be, are aborted or discharged into the water. This not infrequently happens in aquaria, and doubtless may occur in nature. Abortion is presumed to be due to a deficiency of dissolved oxygen in the water; the mussel, beginning to suffocate, discharges the eggs in order to employ its gills more effectively for respiration.

SEASONS OF DEPOSITION OF EGGS.

We must distinguish with fresh-water mussels the seasons when eggs are matured, passed out of the body, and deposited in the marsupial pouches from the season when the developed glochidia are cast out into the water. The term "spawning season" might be misleading, because it is commonly used to refer to the occasion when the glochidia are discharged to the exterior, and this may be weeks, months, or sometimes nearly a year after the eggs are actually extruded from the reproductive organs and the young are launched into existence. In general, the deposition of eggs—the actual spawning process, scientifically speaking—occurs with the long-term breeding class (see below) in the latter part of the summer or early fall. In the short-term breeding class spawning usually takes place in June, July, or August, although in one or two species it is known to occur as early as April. One mussel, the washboard, deposits eggs only in the late summer and early fall, August to October.

It is the experience of the Fisheries Biological Station at Fairport that the spawning seasons of mussels fluctuate to some degree in different years, no doubt because the ripening of mussels is affected by varying conditions of water temperature. There are also, of course, some differences of breeding season corresponding to differing climatic conditions in more northern or more southern waters.

SEASONS OF INCUBATION OF EGGS.

Generally speaking, fresh-water mussels may be divided into two classes with respect to their breeding seasons—the long-term breeders and the short-term breeders.

In the case of the long-term breeders the eggs are fertilized during the middle or latter part of the summer and, passing into the brood pouches, develop into glochidia, which are usually matured by fall or early winter. The glochidia may pass the entire winter in the brood pouches, to be expelled during the following spring and early summer. As might be expected, there is some overlapping of successive breeding seasons; females that have discharged the glochidia quite early in the summer may already have the brood pouches filled with eggs for the next season, while other mussels of the same species are still retaining the glochidia developed from eggs of the past year. This fact is obviously favorable to the work of artificial propagation, rendering it possible to obtain glochidia of certain species of mussels at any time during the year. Thus in Lake Pepin, a widened portion of the Mississippi River between Minnesota and Wisconsin, where the Lake Pepin mucket or fat mucket is being propagated on a large scale by the Bureau, a sufficient number of gravid mussels can be obtained for carrying on the operations from the time they are commenced in May until they are terminated in October or November.

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[a] Exceptions to this rule are noted by Ortmann (1911, p. 299). In such cases (the genera Anodonta, Anodontoides, Symphynota, and Alasmidonta) the eggs or glochidia are entirely separate from one another and flow out freely when the ovisac is opened.

In the case of the short-term breeders the breeding activities are restricted to a season of about five months, from April to August, inclusive. The period of incubation for any individual mussel of this class is undoubtedly very much shorter, although temperature or other conditions may cause the period of incubation to be lengthened or shortened.

In Tables 15 and 16 there are listed the more common species of mussels with indication of the months in which females have been found with mature glochidia. The lack of a record of gravidity may, of course, be due in some cases not to an actual gap in the breeding season but to the want of opportunity for sufficient observation of the species during a particular month. (See also Ortmann, 1909; Lefevre and Curtis, 1912; and Utterback, 1916.)

The commercial and noncommercial species are grouped in different tables, not only because the records are more complete for the former but because those who are concerned with the conduct or regulation of the mussel fishery will be interested almost exclusively in the mussels of direct economic importance.

TABLE 15.—THE MORE IMPORTANT COMMERCIAL MUSSELS, WITH INDICATION OF MONTHS DURING WHICH FEMALES HAVE BEEN FOUND WITH MATURE GLOCHIDIA.

Scientific name.	Common name.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Cyprogenia irrorata	Fan-shell	....	....	....	....	....	....	....	....	....	(?)	x	....
Dromus dromas	Dromedary mussel	....	....	....	....	....	....	....	....	....	x	x	....
Lampsilis anodontoides	Yellow sand-shell	x	x	x	x	x	x	x	x	x	x	x	x
Lampsilis fallaciosa	Slough sand-shell	....	....	....	x	x	x	x	x	x	x	x	x
Lampsilis higginsii	Higgin's eye	....	....	....	....	x	....	....	....	x	....	....	....
Lampsilis ligamentina	Mucket	....	x	x	x	x	x	x	x	x	x	x	x
Lampsilis luteola	Fat mucket	x	x	x	x	x	x	x	x	x	x	x	x
Lampsilis recta	Black sand-shell	....	....	x	x	x	x	x	x	x	x	x	x
Lampsilis ventricosa	Pocketbook	x	x	x	x	x	x	x	x	x	x	x	x
Obliquaria reflexa	Three-horned warty-back	....	....	....	x	x	x	x	x	....	....	....	....
Obovaria ellipsis	Hickory-nut	....	x	....	x	x	x	....	x	x	x	x	x
Plagiola securis	Butterfly	....	x	....	....	x	x	x	x	x	x	x	....
Pleurobema æsopus	Bullhead	....	....	....	....	x	x	x	....	....	....	....	....
Ptychobranchus phaseolus	Kidney-shell	....	....	....	....	....	....	....	x	x	x	x	....
Quadrula cylindrica	Rabbit's foot	....	....	....	....	....	x	x	....	....	....	....	....
Quadrula ebenus	Niggerhead	....	....	....	x	x	x	x	x	x	....	....	....
Quadrula heros	Washboard	x	x	x	....	....	....	....	....	x	x	x	x
Quadrula lachrymosa	Maple-leaf	....	....	....	x	x	x	x	x	....	....	....	....
Quadrula metanevra	Monkey-face	....	....	....	x	x	x	x	....	....	....	....	....
Quadrula obliqua	Ohio River pig-toe	....	....	....	x	x	x	x	x	....	....	....	....
Quadrula perplicata	Round Lake	....	....	....	....	x	x	x	....	....	....	....	....
Quadrula plicata	Blue-point	....	....	....	....	x	x	x	x	....	....	....	....
Quadrula pustulata	Pimple-back	....	....	....	....	....	x	x	....	....	....	....	....
Quadrula pustulosa	do	....	....	....	....	....	x	x	x	....	....	....	....
Quadrula rubiginosa		....	....	....	....	x	x	x	x	....	....	....	....
Quadrula solida		....	....	....	....	x	x	....	....	....	....	....	....
Quadrula undata	Pig-toe	....	....	....	....	....	x	x	x	x	....	....	....
Quadrula undulata	Three-ridge	....	....	....	....	x	x	x	....	....	....	....	....
Symphynota complanata	White heel-splitter	x	....	x	x	x	x	....	....	x	x	x	x
Tritogonia tuberculata	Buckhorn	....	....	....	x	x	x	....	....	....	....	....	....
Unio crassidens	Elephant's ear	....	....	....	x	x	x	....	....	....	....	....	....
Unio gibbosus	Lady-finger	....	....	....	....	x	x	x	x	....	....	....	....

TABLE 16.—SOME NONCOMMERCIAL MUSSELS, WITH INDICATION OF MONTHS DURING WHICH FEMALES HAVE BEEN FOUND WITH GLOCHIDIA.

Scientific name.	Common name.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Alasmidonta marginata	Elk-toe									x			
Anodonta cataracta												x	
Anodonta corpulenta	Slop-bucket	x			x						x	x	
Anodonta grandis	Floater	x	x	x						(?)			x
Anodonta imbecillis	Paper-shell	x	x	x		x	x	x	x	x	x	x	x
Anodonta implicata										x	x		
Anodonta stewartiana												x	
Anodonta suborbiculata	Paper-shell	x	x										x
Arcidens confragosus	Rock pocketbook	x								x		x	
Gonidea angulata							x						
Hemilastena ambigua										x	x		
Lampsilis alata	Pink heel-splitter	x	x	x		x	x	x	x	x	x	x	
Lampsilis borealis										x			
Lampsilis capax	Pocketbook						x	x	x	x			
Lampsilis gracilis	Paper-shell	x	x		x	x	x	x	x		x	x	x
Lampsilis iris	Rainbow-shell						x						
Lampsilis ellipsiformis						x	x						
Lampsilis lævissima	Paper-shell	x		x	x		x	x	x	x		x	
Lampsilis lienosa						x				x			
Lampsilis parva							x						
Lampsilis subrostrata							x			x			
Lampsilis texasensis						x							
Lampsilis ventricosa satura						x	x						
Plagiola donaciformis						x		x					
Plagiola elegans	Deer-toe					x		x					
Ptychobranchus phaseolus	Kidney-shell								x				
Quadrula cooperiana							x	x	x				
Quadrula granifera	Purple warty-back							x					
Strophitus edentulus	Squaw-foot			x	x	x	x		x	x	x	x	
Symphynota costata	Fluted shell									x	x		
Symphynota compressa										x			
Truncilla arcæformis	Sugar-spoon										x		
Truncilla capsæformis	Oyster mussel										x		
Unio tetralasmus						x							

It will be observed that, generally speaking, the several species of Quadrula and Unio, as well as *Pleurobema æsopus* (bullhead), *Tritogonia tuberculata* (buckhorn), and *Obliquaria reflexa* (three-horned warty-back) are short-term breeders, while the species of Lampsilis, as well as *Obovaria ellipsis* (hickory-nut), and *Symphynota complanata* (white heel-splitter), *Plagiola securis* (butterfly), and others are long-term breeders. Most interesting is the case of the washboard, *Quadrula heros*, which, from its taxonomic position, would be expected to have the short summer breeding season, but which at least simulates the long-term breeders. The glochidia become mature from early autumn to winter, apparently varying with the latitude, but so far as known are not held for a long period after maturity. They react like the short-term summer breeders when removed from the water in that they quickly abort the contained glochidia. It may be either that its relationship has been incorrectly appraised or that it represents a transition stage from the short-term to the long-term breeding class. Certainly it is the one species of mussel subjected to close study which has never been found to have either eggs or glochidia in its gills during the summer months.

Finally, it may be remarked that the terms "short-term" and "long-term," as applied to the breeding season, are perhaps inappropriate and misleading. So far as we know, in all species (except the washboard, in one respect) the development of the egg into the glochidium follows promptly on ovulation, occupies a period of a very few weeks, and occurs during warm weather. The short-term breeders are those which throw out the glochidia at once, while the long-term breeders carry them over until the following year. It seems to be a general rule that the short-term breeders pass through all phases of reproductive activity on a rising temperature, while the long-term breeders begin their breeding activities on falling temperatures of one season, but discharge the glochidia on rising temperatures of the following season.

Several experiments have shown that the glochidia taken from long-term breeders in the fall of the year may be successfully infected upon fish and that the young mussels will undergo development. It appears, however, that these "green" or newly formed glochidia require a longer period of parasitism than those which have been nursed by the parent through the winter season (Corwin, 1920).

The origin and purpose of the retention of glochidia during the winter season remains a mystery. This may be an instance of nature's remarkable adaptations, permitting the development of the egg to occur during the warmer months of summer, and the glochidia to be discharged for attachment upon fish in the spring when there is a general tendency toward an upstream movement of fishes. It is distinctly interesting to note that the long-term breeders (mucket, sand-shells, etc.), as a general rule are mussels of much more rapid growth than the short-term breeders (niggerhead, pimple-back, etc.), although the young of the former are delayed for nearly a year in becoming attached to fish and completing their metamorphosis.

It is important to point out one fact which is clearly established by data in Table 15, page 141. There is no month of the year in which a considerable number of commercial mussels are not gravid with glochidia. This fact deserves careful consideration in connection with measures of conservation, since it makes impracticable the protection of mussels by "closed seasons" of months based upon the times of breeding.

GLOCHIDIUM.

The larval mussel or glochidium, when completely developed and ready to emerge from the egg membrane and before attaching itself to a fish, has apparently an extremely simple organization. The soft mass of flesh possesses neither gills nor foot nor other developed organ characteristic of the adult mussel, but it bears a thin shell composed of two parts which are much like the bowls of tiny spoons hinged together at the top (text fig. 8). The two parts or valves of the shell can be drawn together by a single adductor muscle, but, when the muscle is relaxed, they gape widely apart as shown in the illustration. There are also on the inner surface of each side of the body several pairs of "sensory" cells with hairlike projections. It has been assumed that the cells were sensory in function, and recently L. B. Arey, working at the Fairport station, determined after detailed experiments upon several species of Lampsilis and Proptera that there is a well-developed sense of touch centralized in the hair cells. He regards the tactile response as entirely adequate to insure attachment of the glochidium.

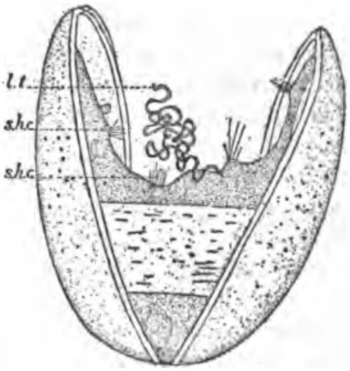

Fig. 8.—Glochidium of *Quadrula heros* with gaping valves, seen from a side view. The larval thread (*l. t.*) is seen between the valves. Inner and outer sensory hair cells (*s. h. c.*) are visible on each valve.

In at least three genera of American mussels (several species of Unio, Anodonta, and Quadrula) the glochidium possesses a peculiar larval thread of uncertain significance (text fig. 8). This thread, so generally mentioned in textbooks based upon studies of European mussels, is not found on the great majority of American species. We have observed it on glochidia of the following species: The washboard, *Quadrula heros*, the blue-point, *Q. plicata*, the pig-toe, *Q. undata*, the bullhead, *Pleurobema æsopus*, the spike, *Unio gibbosus*, the slop-bucket, *Anodonta corpulenta*, and the river pearl mussel, *Margaritana margaritifera*. The squaw-foot, *Strophitus edentulus*, has a modified larval thread (Lefevre and Curtis, 1912, p. 173).

That the structure of the glochidium is less simple than appears to the ordinary observer is shown by the fact that, in the fully developed glochidium, close microscopic study will reveal the rudiments of foot, mouth, intestine, heart, and other organs which will not, however, assume their destined form and functions until after the period of parasitism. The shell of the glochidium is firm but somewhat brittle owing to the carbonate of lime of which it is partly composed. If the lime is dissolved out with acid, the remaining shell, composed only of cuticle, preserves its general form, although it becomes wrinkled and collapsible.

The number of glochidia borne in the brood pouches of a fully grown female mussel according to the counts and computations made by various observers, varies in the different species from about 75,000 to 3,000,000. An example of the paper-shell, *Lampsilis gracilis*, yielded by computation 2,225,000 glochidia. The mussel was 7.4 cm. (about 3 inches) in length. Several examples of the Lake Pepin mucket yielded glochidia in the following numbers, the length of the mussel being indicated in parentheses: (6.1 cm.) 79,000; (7 cm.) 74,000; (7.4 cm.) 125,000; (8.5 cm.) 129,000.

The glochidia of mussels are very diverse in size and form, although for any given species the dimensions and shape of the glochidium have been regarded as fairly constant (Surber, 1912 and 1915). Differences in sizes of glochidia within the species are noted by Ortmann (1912 and 1919)[a] and Howard (1914, p. 8). The matter requires investigation. As regards their form, glochidia are separable into three well-known types: (1) the "hooked" type, (2) the "hookless" or "apron" type, and (3) the "ax-head" type.

(1) The "hooked" type (Pl. XIV, figs. 1 and 2) possesses a rather long stout hinged hook at the ventral margin of each triangular or shield-shaped valve. These glochidia are usually larger than those of the other two types and the shell is considerably heavier. The hooks are provided with spines which no doubt assist the glochidium in retaining its hold upon the host. As all hooked glochidia generally (though not invariably) attach to the exterior and exposed parts of the fish, the fins and scales, the advantage of the heavier shell and stout hooks may readily be seen. This type of glochidium is possessed by mussels of the genera Anodonta, Strophitus, and Symphynota (floaters, squaw-foot, and white heel-splitter, etc.). (See also text figs. 9 and 12.)

(2) The shells of glochidia of the "hookless" type (Pl. XIV, figs. 3, 4, and 5), while lighter than those of the hooked type, are nevertheless of sufficient strength to withstand considerable rough handling. So far as we now know, all the glochidia of this type are gill parasites with the exception of the washboard, *Quadrula heros*, which has been successfully carried through the metamorphosis on both gills and fins. The hookless glochidia vary rather widely in shape and in size (text figs. 9 to 12); among the smallest is that of the spectacle-case, *Margaritana monodonta* (0.05 by 0.052 mm).; while one of the largest is that of the purple pimple-back, *Quadrula granifera* (0.290 by 0.355 mm.). Placed side by side, about 500 of the smallest or about 80 of the largest

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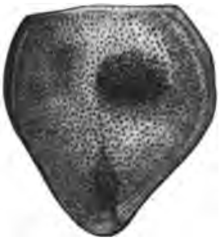
[a] Ortmann gives many cases of small discrepancies between his measurements and those of others, based no doubt upon the different sources of material. In several cases he has observed differences in sizes of glochidia from different individuals. See papers in the Nautilus, Vol. XXVIII, 1914, and Vol. XXIX, 1915. In one instance he reports glochidia of two sizes from one individual (1912, p. 353). See also Surber, 1912, p. 4.

PLATE XIV.



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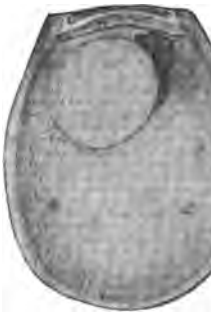

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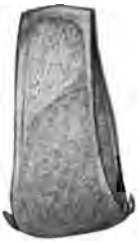

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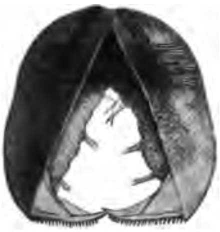

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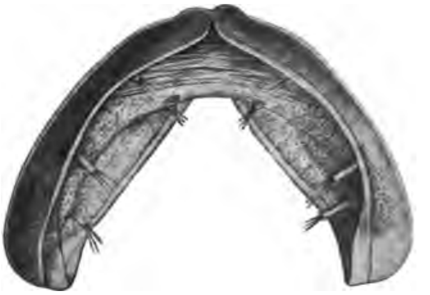

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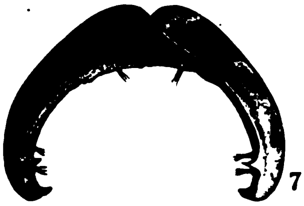

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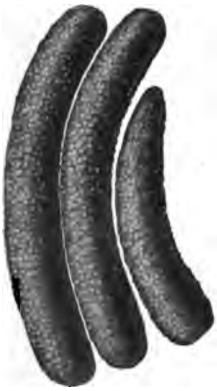

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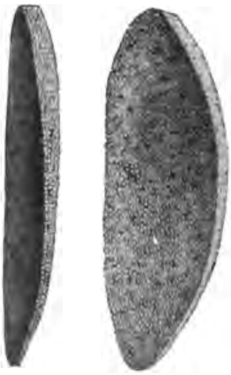

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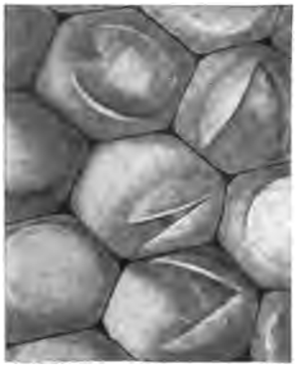

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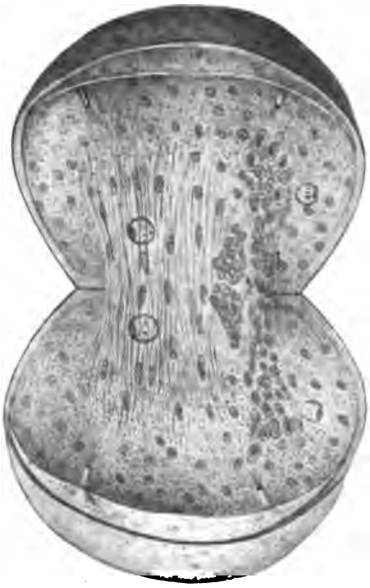

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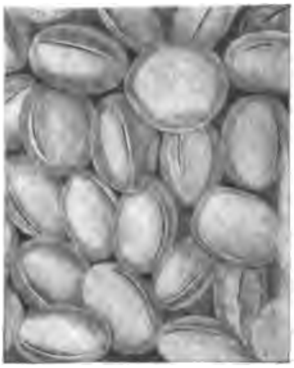

11

[Figures from Lefevre and Curtis, 1912.]

FIGS. 1 and 2.—Hooked glochidium of *Symphynota costata*.

FIGS. 3, 4, and 5.—Hookless glochidium of *Lampsilis subrostrata*.

FIGS. 6 and 7.—Ax-head glochidium of *Lampsilis* (*Proptera*) *alata*.

FIG. 8.—Conglutinates (masses of glochidia) from the three-horned warty-back, *Obliquaria reflexa*.

FIG. 9.—Portion of conglutinate of *Obliquaria reflexa*, magnified. Glochidia still within egg membranes which are closely pressed and adhering together.

FIG. 10.—Conglutinates (masses of glochidia) from the mucket, *Lampsilis ligamentina*.

FIG. 11.—Portion of conglutinate of *Lampsilis ligamentina* magnified. Glochidia inclosed in membranes are embedded in a mucilaginous matrix.

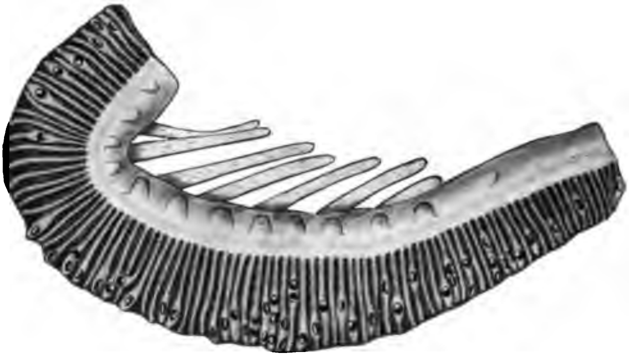

FIG. 1.—Gill of a black bass infected with glochidia of mucket, *Lampsilis ligamentina*.

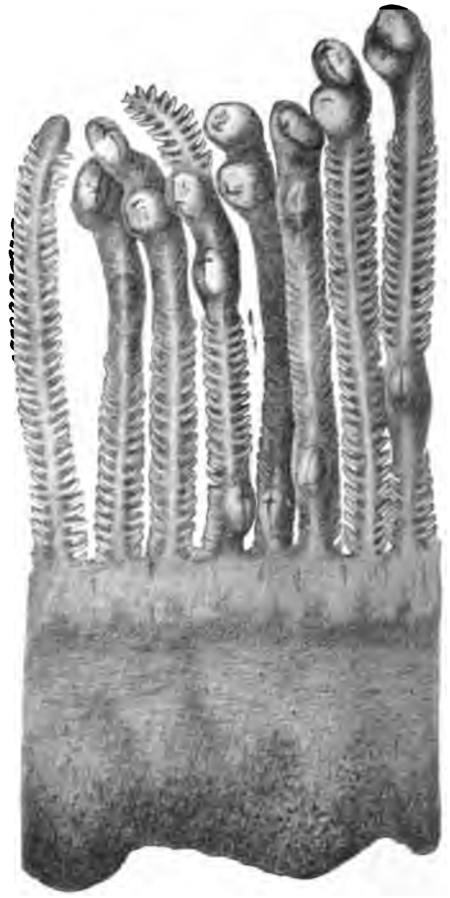

FIG. 2.—Part of fig. 1, enlarged.

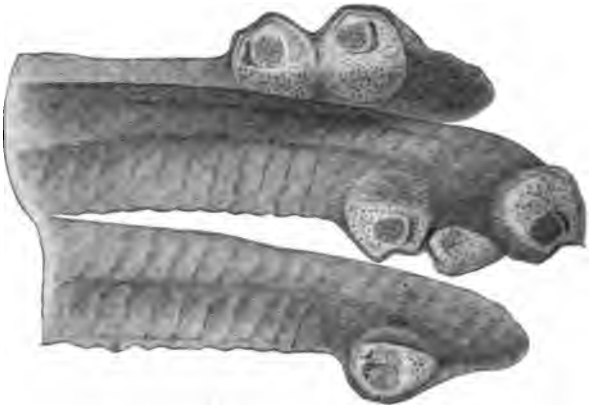

FIG. 3.—Three gill filaments of rock bass, with glochidia of mucket.

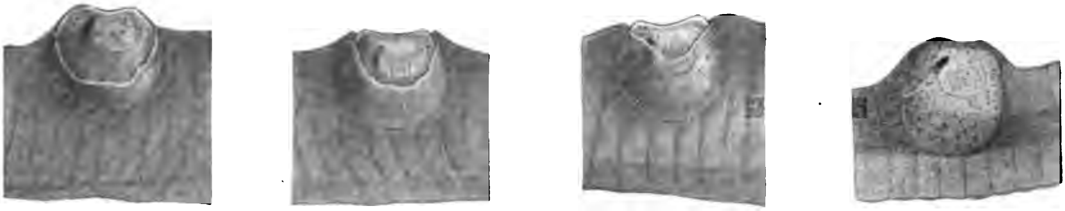

FIG. 4.—Stages in formation of cyst surrounding a glochidium of the mucket. Taken at 15 minutes, 30 minutes, 1 hour, and 3 hours, respectively, after infection.

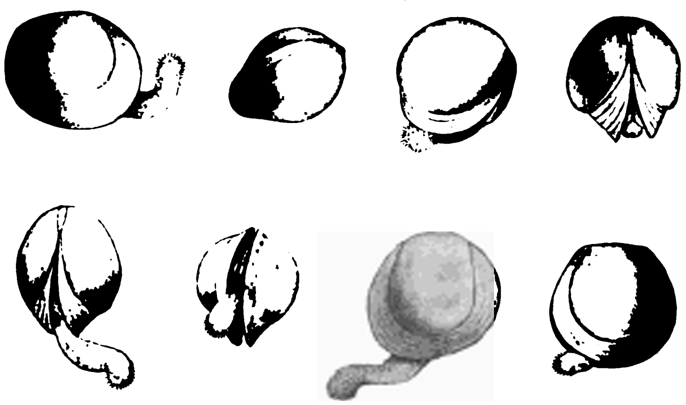

FIG. 5.—Young muckets, one week after liberation from the fish, showing new growth of shell, cilia on foot, and positions assumed in crawling. Enlarged.

FIG. 6.—Young Lake Pepin muckets at ages of 1, 2, 3, and 4 months, respectively. Natural size.

[Figs. 1–5 after Lefevre and Curtis.

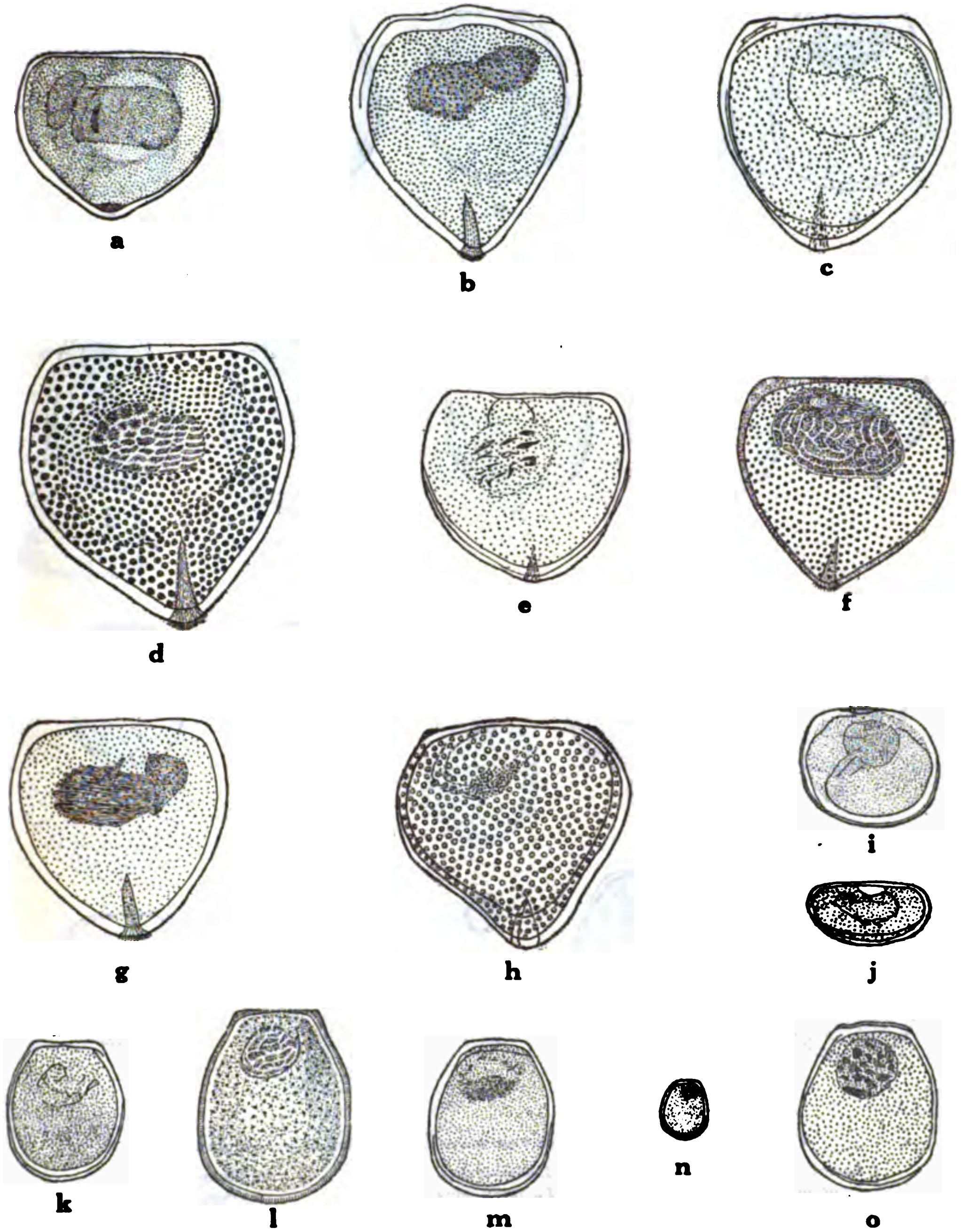

FIG. 9.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a, Alasmidonta calceola.
b, Alasmidonta marginata.
c, Anodonta corpulenta.
d, Anodonta grandis.
e, Anodonta imbecillis.
f, Anodonta suborbiculata.
g, Anodontoides ferussacianus subcylindraceus.
h, Arcidens confragosus.
i, Cyprogenia irrorata.
j, Dromus dromas.
k, Lampsilis anodontoides.
l, Lampsilis breviculus brittsi.
m, Lampsilis fallaciosa.
n, Lampsilis gracilis.
o, Lampsilis higginsii.

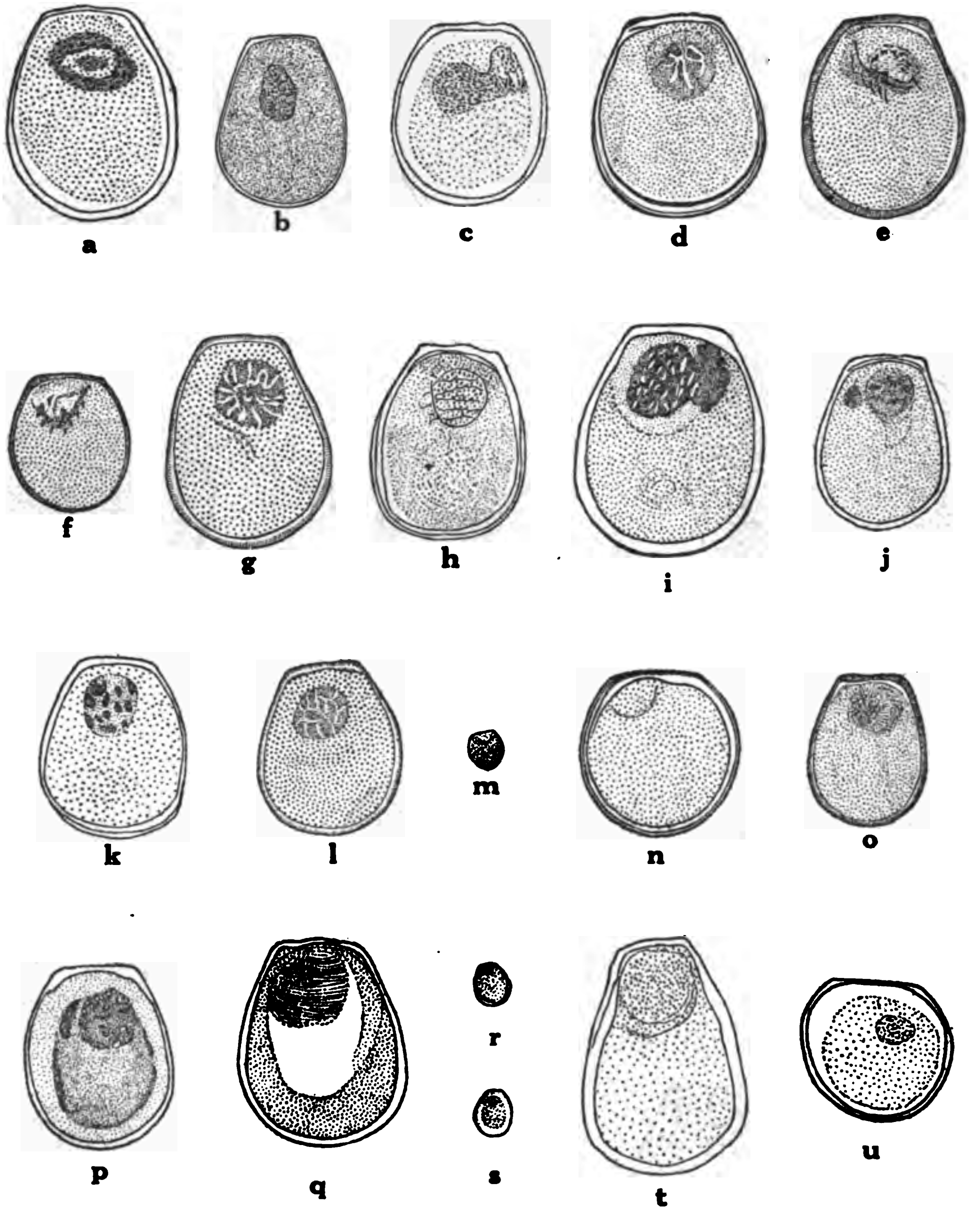

FIG. 10.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a, *Lampsilis iris.*
b, *Lampsilis lienosa unicostata.*
c, *Lampsilis ligamentina.*
d, *Lampsilis luteola.*
e, *Lampsilis multiradiata.*
f, *Lampsilis parva.*
g, *Lampsilis picta,*
h, *Lampsilis recta.*
i, *Lampsilis subrostrata.*
j, *Lampsilis trabalis.*
k, *Lampsilis ventricosa.*
l, *Lampsilis ventricosa satura.*
m, *Margaritana monodonta.*
n, *Obliquaria reflexa,*
o, *Obovaria circulus.*
p, *Obovaria ellipsis.*
q, *Obovaria retusa.*
r, *Plagiola donaciformis.*
s, *Plagiola elegans.*
t, *Plagiola securis.*
u, *Pleurobema æsopus,*

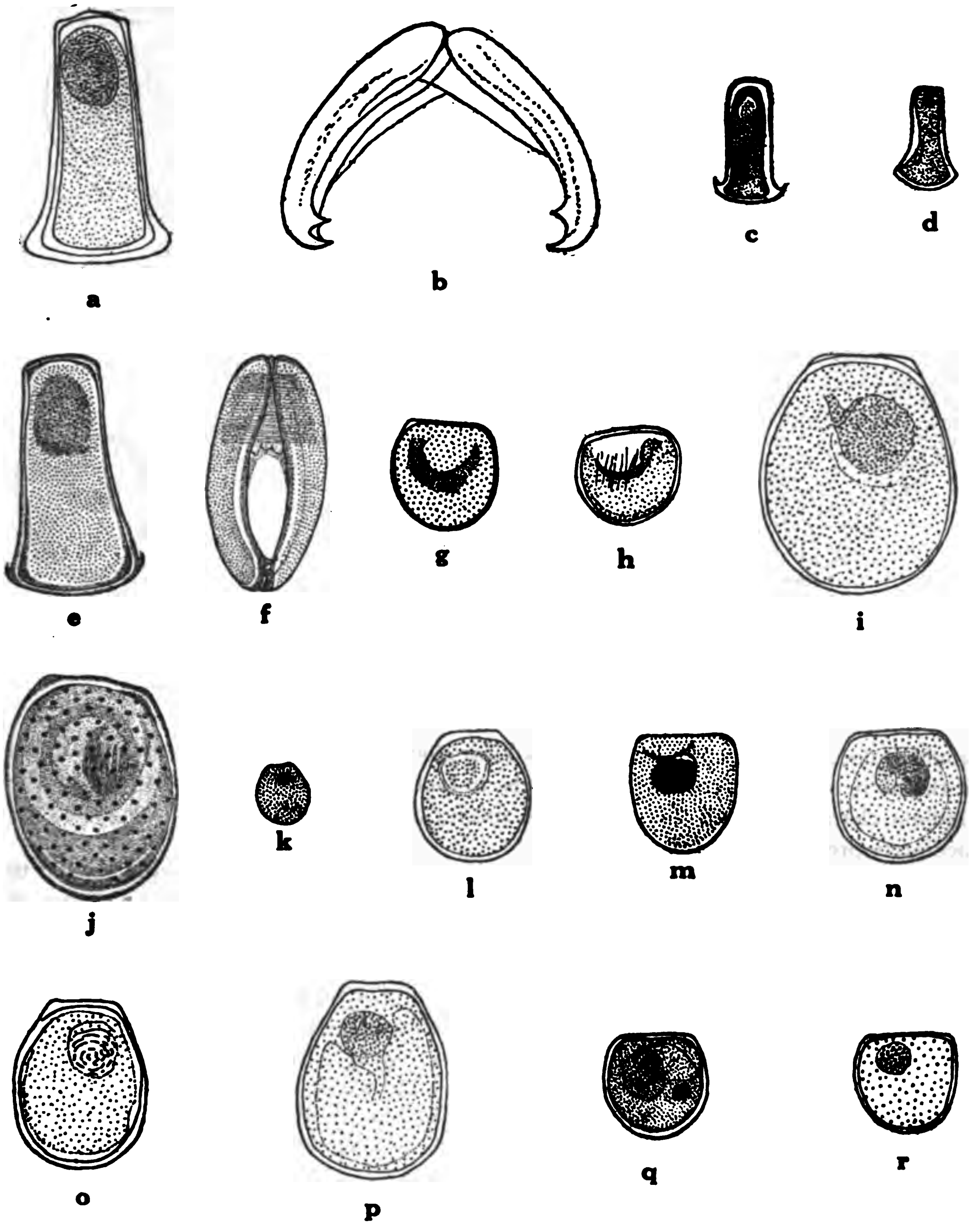

FIG. 11.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a and *b*, *Proptera alata.*
c, *Proptera capax.*
d, *Proptera laevissima.*
e and *f*, *Proptera purpurata.*
g, *Quadrula coccinea.*
h, *Quadrula ebenus*,
i, *Quadrula granifera.*
j, *Quadrula heros.*
k, *Quadrula lachrymosa.*
l, *Quadrula metanevra.*
m, *Quadrula obliqua.*
n, *Quadrula plicata.*
o, *Quadrula pustulata.*
p, *Quadrula pustulosa.*
q, *Quadrula solida.*
r, *Quadrula undata.*

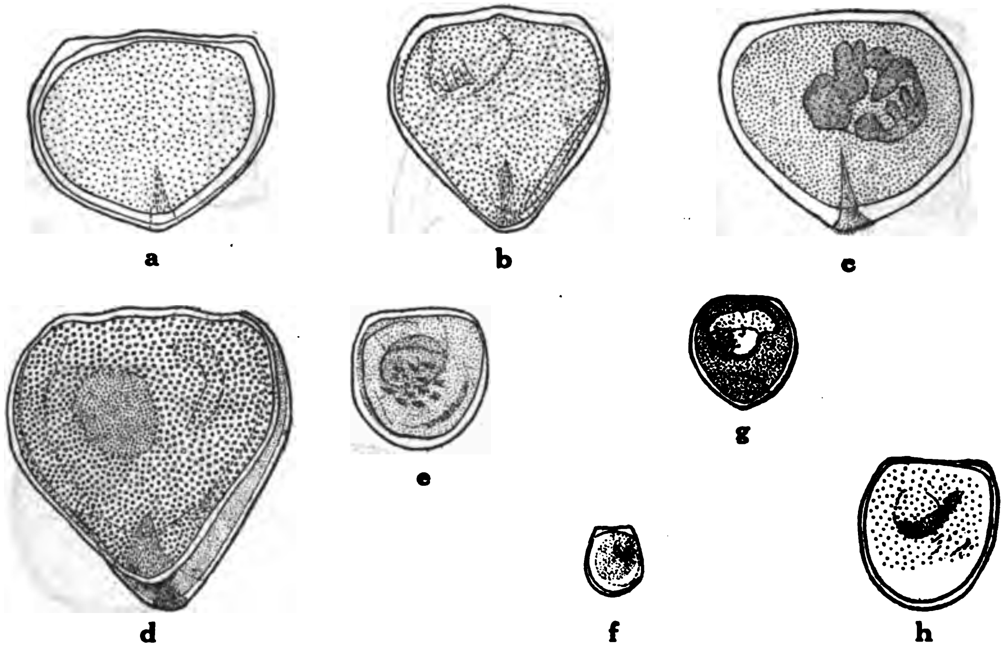

FIG. 12.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a, Strophitus edentulus.
b, Symphynota complanata.
c, Symphynota compressa.
d, Symphynota costata.
e, Truncilla sulcata.
f, Tritogonia tuberculata.
g, Unio crassidens.
h, Unio gibbosus.

would make a line 1 inch in length. Hookless glochidia are possessed by practically all of the more important commercial mussels; in fact, as far as we know, this type of glochidium characterizes all the genera and species not mentioned in the paragraphs immediately preceding and following.

(3) The "ax-head" type (Pl. XIV, figs. 6 and 7) is considered more closely related to the hookless than to the hooked type, although glochidia of this type, except those of a single species, *Lampsilis* (*Proptera*) *lævissima* (Coker and Surber, 1911), possess four hooklike prongs, one at each lower corner of the shell. These pointed projections of the shell are not comparable to the pivoted hooks of glochidia of the hooked type. The ax-head type of glochidium occurs with the following species: *Lampsilis* (*Proptera*) *alata*, *lævissima*, *purpurata*, and *capax*. (See also text fig. 11, a to f.)

When the glochidia are fully developed they are ready to break out from the egg membrane and to be liberated from the gills of the mussel, although as previously indicated many species of mussels retain the developed glochidia in their gills for many months. A characteristic feature of the mature and healthy glochidium is the active snapping together and opening of the shell. This action can be stimulated by adding a drop of fish blood or a few grains of salt to the water in which the glochidia are held.

STAGE OF PARASITISM.

After the fully matured glochidium has been expelled from the brood pouch of the mother, its continued development is dependent upon its coming in contact with the gills or fins of a suitable fish host and attaching to them. If it fails to make this attach-

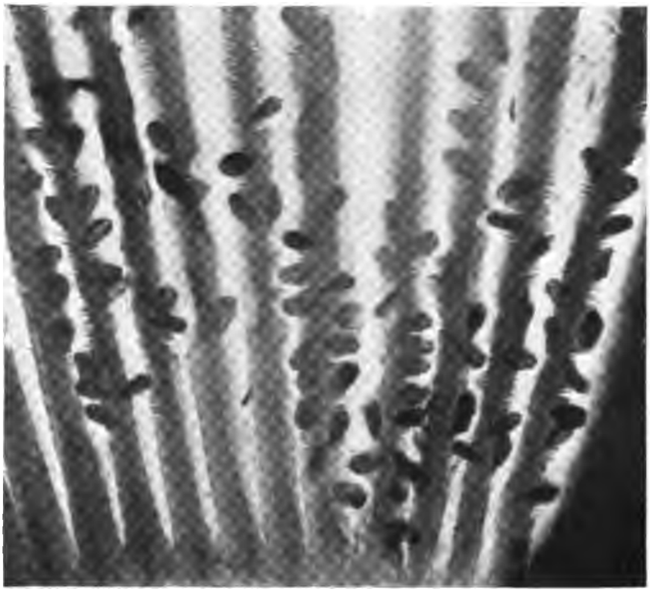

FIG. 1.—Filaments of gill of fresh-water drum with heavy natural infection of *Plagiola donaciformis*. Estimated total number of glochidia carried by fish 4,800.

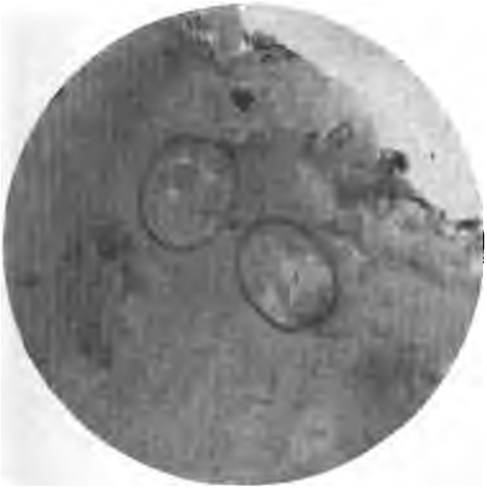

FIG. 2.—Glochidia of washboard mussel, *Quadrula heros*, on fin of fresh-water drum. Cyst very much enlarged.

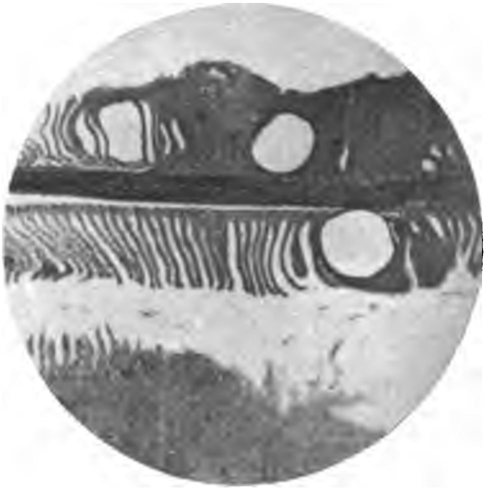

FIG. 3.—Section through vacated cysts on gill filaments; *Quadrula ebenus* on river herring.

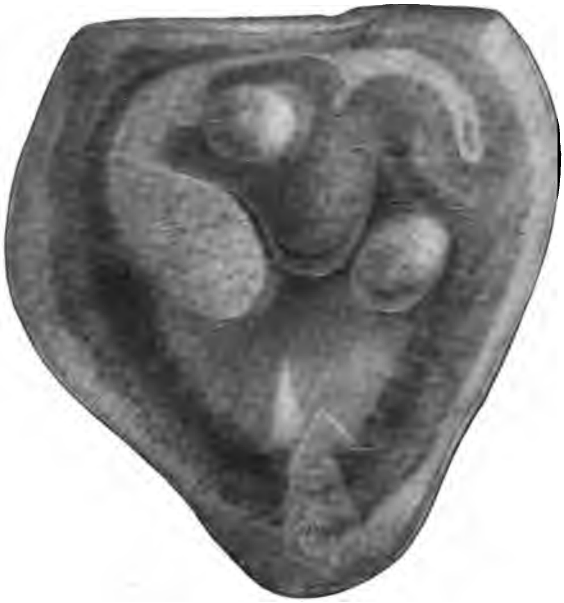

FIG. 1.—Glochidium of *Symphynota costata* in process of transformation during stage of parasitism. (Lefevre and Curtis.)

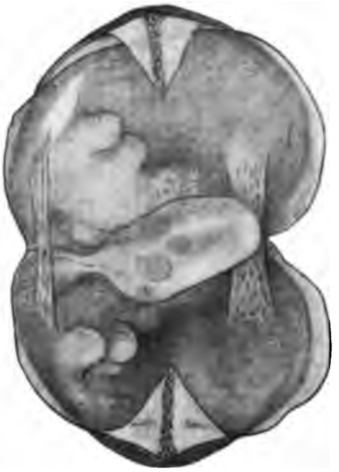

FIG. 2.—A young mussel, *Symphynota costata*, six days after completing the stage of parasitism. (Lefevre and Curtis.)

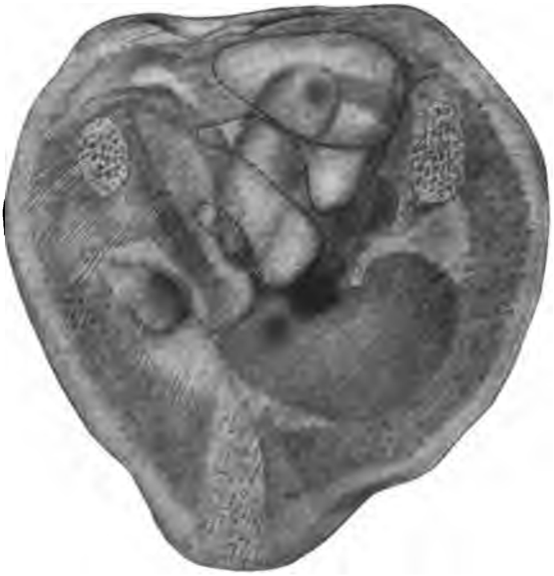

FIG. 3.—A young squaw-foot mussel, *Strophitus edentulus*, which had completed metamorphosis without parasitism; showing two adductor mussels, foot, gills, and rudiments of other organs of adult mussel. (Lefevre and Curtis.)

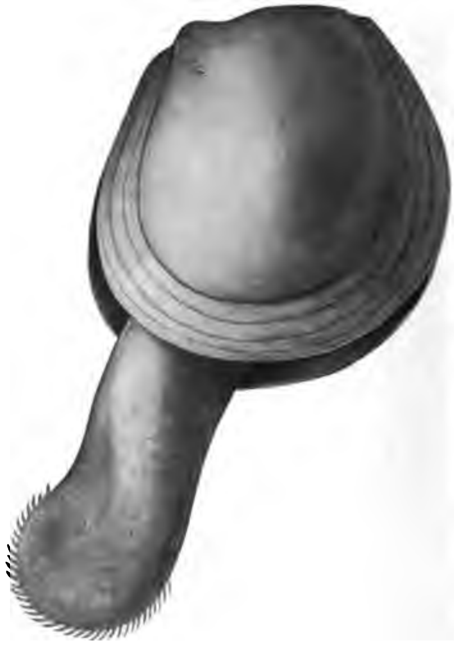

FIG. 4.—A young mucket, *Lampsilis ligamentina*, a week after the close of the parasitic period. (Lefevre and Curtis.)

ment it will die within a few days' time. In other words, the glochidium must pass the life of a virtual parasite on the fish while undergoing its metamorphosis into the free-living juvenile stage. In the light of our present knowledge, this is true of all the fresh-water mussels (Unionidæ) except the squaw-foot, *Strophitus edentulus*, and one of the small floaters, *Anodonta imbecillis*. The former species may complete its metamorphosis either with or without parasitism (Lefevre and Curtis, 1911 and 1912, p. 171; and Howard, 1914, p. 44), while the latter, as it appears, never endures a condition of parasitism (Howard, 1914, p. 44).

On coming in contact with the gill filament or fin of the fish the glochidium attaches itself by firmly clamping its valves to the tissue of the host. A certain portion of the tissue of the fish thus becomes inclosed within the mantle space of the glochidium, and this quickly disintegrates and is taken into the cells of the glochidium and consumed as food (Lefevre and Curtis, 1912, p. 169). Within a very short time the tissue of the fish commences to grow over the glochidium, presumably in an effort to heal the slight wound caused by the "bite" of the glochidium, or perhaps as the result of a positive stimulus imparted by the glochidium. L. B. Arey (report in preparation) successfully induced encystment by attaching to the filaments of excised gills of fish minute metallic clamps the size of glochidia or smaller. The growth of tissue continues until the larval mussel is completely inclosed within a protective covering known as the cyst (Pl. XVI, fig. 2). The several stages of encystment are clearly represented in the series of figures reproduced from Lefevre and Curtis (1912) (Pl. XV, fig. 4), and the process may be completed within 24 or 36 hours. The appearance of a gill bearing a considerable number of glochidia is shown by figure 1 of Plate XV, while figure 2 is an enlarged view of a few of the gill filaments of a black bass carrying glochidia of the mucket.

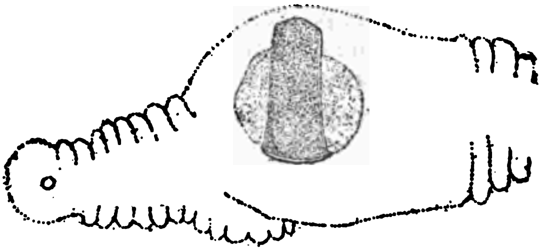

FIG. 13.—Glochidium of pink heel-splitter, *Lampsilis* (*Proptera*) *alata*, in condition of parasitism on gill of sheepshead, showing growth of the juvenile mussel beyond the bounds of the glochidial shell.

It is not our purpose to go in detail into the changes which occur in the glochidium during the period of its parasitism. They are principally changes of internal structure which scarcely affect the external appearance. Nevertheless, at the conclusion of parasitic life the young mussel is a very different sort of an organism from the simply organized glochidium which has been described on page 143. Generally it has not increased in size, but the single muscle which held the valves of the glochidial shell together has given place to two adductor muscles as in the adult; the mouth and the intestine are formed, the gills and foot are represented by rudiments which are prepared to function. The larval mussel is, in fact, ready to begin its independent life and to take care of itself. All of the changes which occur during parasitism require the expenditure of energy and the use of body-building material, and as the glochidium enters upon the parasitic life with no considerable store of food material, it is reasonable to assume that it derives at least a small amount of nutritive material from the fish. Since no growth in size generally occurs, the drain upon the fish therefore must be comparatively slight. There are, however, a few species (none of the commercial mussels, so far as we know) in which, during the period of metamorphosis, the larval mussel grows to a comparatively large size (text fig. 13), and, in such cases, the mussel must be generously nourished by the fish. (See Coker and Surber, 1911.)

The duration of the parasitic period varies greatly with the season of the year during which it occurs, and with other conditions which are not fully understood. The results of some recent experiments indicate that glochidia of long-term breeders have a relatively long infection period when they are infected upon fish shortly after maturing and a relatively short period when infected after they have remained in the marsupial pouches over winter; that is, young glochidia complete metamorphosis in parasitism more slowly than old glochidia. The temperature of the water seems to be one of the factors governing the duration of the parasitic period, and doubtless the vitality of the host fish is another; but there is diversity even among glochidia of the same species when infected on the same fish. Lefevre and Curtis (1912, p. 168), for example, show under such circumstances variations from 9 to 13 days, and even from 13 to 24 days. The following instances (Table 17) from records at the Fairport station are illustrative:

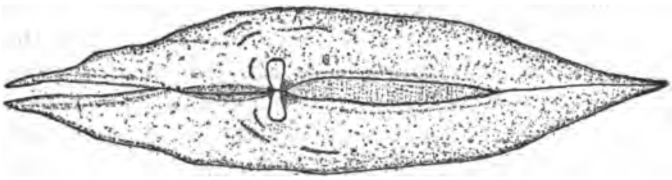

FIG. 14.—A dorsal view of a juvenile pink heel-splitter showing glochidial shell still visible. (×18).

TABLE 17.—INFECTIONS SHOWING DURATION OF PARASITIC PERIOD.

Species of mussel.	Species of fish.	Date of infection.	Duration of infection in days.	Average water temperature during period.
Lampsilis anodontoides	Lepisosteus osseus	June 5, 1919	13	...
Do	do	June 20, 1919	12	...
Do	do	July 3, 1919	11	...
Do	do	July 9, 1919	13	...
Do	do	July 23, 1919	12	...
Lampsilis luteola	Micropterus salmoides	June 5, 1919	13	...
Do	do	June 20, 1919	13	...
Do	do	July 14, 1919	10	...
Do	do	do	11	...
Do	do	do	12	...
Do	do	July 25, 1919	10	...
Do	do	do	12	...
Do	do	do	12	...
Do	do	Aug. 21, 1919	12	...
Do	do	do	11	...
Do	do	Aug. 22, 1919	10	...
Lampsilis ligamentina	do	June 5, 1919	15	...
Do	do	June 30, 1919	13	...
Do	do	do	14	...
Lampsilis luteola	Micropterus dolomieu	July 2, 1914	19	...
Do	Stizostedion vitreum	do	20	...
Do	Perca flavescens	Aug. 18, 1914	68	...
Do	do	Sept. 26, 1914	(a)	...
Do	Stizostedion vitreum	Sept. 16, 1914	(a)	...
Quadrula pustulosa	Ameiurus melas	Aug. 21, 1912	6 to 8	75.1
Do	Ictalurus punctatus	July 7, 1912	9 to 11	78.1
Do	do	Aug. 4, 1912	11 to 12	75.5
Quadrula plicata	Lepisosteus platostomus	July 12, 1918	11	76.5
Lampsilis fallaciosa	do	July 13, 1918	14 to 18	78.3
Lampsilis anodontoides	do	July 7, 1919	14 to 21	74.6
Quadrula heros	Aplodinotus grunniens	Oct. 7, 1912	193	43.3 ca.

[a] Still carrying infection, Apr. 14, 1915.

In about one week after attachment, as a rule, the wall of the cyst begins to assume a looser texture, the intercellular spaces becoming infiltrated with lymph, and from this time on to the end of the parasitic period there is little further change in its structure.

Before liberation of the young mussel, the valves open from time to time and the foot is extended. By the movements of the latter the cyst is eventually ruptured, its walls gradually slough away, and the mussel thus freed falls to the bottom (Lefevre and Curtis, 1912, p. 171).

Before taking up the history of the mussels in independent juvenile life, we must discuss the very significant facts which have been discovered concerning the special relation between mussel species and fish species, and refer also to the rare instances known of mussels which complete their development without the aid of fish.

HOSTS OF FRESH-WATER MUSSELS.

As has previously been indicated in a general way, mussels do not attach to fish indiscriminately, but for each species there is a restricted choice of hosts. Some are more catholic in their tastes than others, yet for any mussel there is a limited number of species of fish upon which it will attach and complete its metamorphosis. The Lake Pepin mucket has nine known hosts, while the niggerhead has apparently but one; the yellow sand-shell is restricted to gars, and the pimple-back to catfishes. It is, of course, employing language in a loose sense to refer to this selection of hosts in terms of taste or choice; it is a matter of physiological reaction. When fish and glochidia are artificially brought together, glochidia will sometimes attach to the wrong fish, but in such cases they soon drop off, or even if partial or complete encystment ensues, the glochidium does not develop normally and after a time cyst and glochidium are sloughed off and lost. It seems evident, then, that successful encystment and development depend upon appropriate reactions on the part of both glochidium and fish, and that failure ensues upon the lack of a favorable reaction on the part of either parasite or host. The reaction may depend in part upon the condition of the individual glochidium or fish, but primarily it depends upon the species of mussel and the species of fish.

It is evident that the artificial propagation of mussels can not be conducted successfully and economically unless we have accurate knowledge of what species of fish serve as hosts for the several species of mussels. Such knowledge has been gained by following two methods of inquiry, the observational and the experimental.

By the observational method, fish taken in the rivers are subjected to careful examination for the presence of glochidia on the gills or fins. Preliminary to and attendant on such studies, glochidia have been taken from as many species of mussels as could be found in gravid condition, these have been studied with the microscope, measured, and figured, so that in most cases the species of mussel can be identified in the glochidium stage as well as in the adult. (See text figs. 9 to 12.) This method of determining the natural hosts is exceedingly laborious. Infection in nature is a matter of chance, and only a small proportion of fish bear infections. If it were otherwise, artificial propagation might not be necessary. One must, therefore, examine large numbers of fish from different localities and at different seasons, and even then the glochidia of some species may not be encountered, or they may not be found upon all the hosts to which they are adapted. During the calendar year 1913, for example, 3,671 fish of 46 species were examined for natural infections principally during the warmer months from April to October. Of these, 324, or 8.9 per cent, were found to be infected with glochidia of some species, but only 104 of these, or less than 3 per cent, were infected with glochidia of commercial species of mussels. The fishes infected with commercial mussels belonged to 12 species, and the glochidia represented 20 species. The average number of glochidia of a given species on infected fish ran from 1 to 416, with a mean of 125.[a]

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[a] In August, 1912, 5 examples of the river herring were taken and found to bear glochidia of niggerhead mussels in numbers ranging from 1,895 to 3,740 per fish (Surber, 1913, p. 110). Similarly, heavy infections are frequently found on the fresh-water drum, but the glochidia are not usually those of commercial mussels.

The experimental method is simpler in some respects. It consists in submitting various species of fish to infection with the glochidia of a given species of mussel and observing whether or not the glochidia attach. Since glochidia will sometimes attach to fish which are not their natural hosts, it is necessary to hold the fish under observation until the mussels have completed the metamorphosis and dropped off. It is, however, impracticable to have on hand all the species of fish at the particular time when the glochidia of a given species of mussel may be available. Furthermore, the failure of an artificial infection to go through successfully on fish held in confinement may be due, not to the want of a natural affinity between mussel and fish, but to the fact that the fish does not retain its full vitality in close confinement, or to some other defect in the experimental conditions. Neither of the two methods for the study of infections may, then, be relied upon exclusively for the determination of the natural hosts of fresh-water mussels. On the contrary, it has been found necessary to carry on the two lines of study hand in hand, according to the plan which was adopted at the beginning of the scientific work of the station. In this way, though our knowledge of the hosts of mussels is as yet incomplete, there has been obtained a considerable body of information most of which is summarized in the following table (18),[a] listing 17 species of mussel and 30 hosts (29 fishes and 1 amphibian), and indicating those which serve as hosts for each species of mussel.

EXPLANATION OF TABLE 18.

N. Found on the gills in natural infection.
Nf. Found on the fins in natural infection.
n. Record of natural infection but of doubtful significance.
A. Carried through on gills after artificial infection.
Af. Carried through on fins after artificial infection.
a. Results of artificial infection unsatisfactory or not uniform.
o. Tested and found unsuitable.
T. Tested; development occurred; host perhaps suitable, but experiment not carried to conclusion.

TABLE 18.—COMMERCIAL MUSSELS AND THEIR HOSTS.

Mussels.																	
Scientific name.	Common name.	A. melas, bullhead.	A. nebulosus, bullhead.	A. calvus, bowfin.	A. chrysypa, eel.	A. grunniens, sheepshead.	D. cepedianum, gizzard shad.	E. lucius, pike.	E. gibbosus, red-ear sunfish.	H. tergisus, mooneye.	I. punctatus, spotted cat.	L. osseus, long-nosed gar.	L. platostomus, short-nosed gar.	L. tristoechus, alligator gar.	L. cyanellus, blue-spotted sunfish.	L. euryorus, sunfish.
Lampsilis anodontoides	Yellow sand-shell	o	o	a		o					o	AN	A	A	no	
Lampsilis fallaciosa	Slough sand-shell										o		NA			o
Lampsilis higginsii	Higgin's eye					n										
Lampsilis ligamentina	Mucket	o	o	o	n	o		a			o		a		N	
Lampsilis luteola	Fat mucket	o	o			o				o	o		o			
Lampsilis recta	Black sand-shell				n						o				a	
Lampsilis ventricosa	Pocketbook															
Obovaria ellipsis	Missouri niggerhead					o					o					
Plagiola securis	Butterfly					NA									n	
Quadrula ebenus	Niggerhead	o	o	o		o	a			o	o				o	
Quadrula heros	Washboard	A	A		N	AfNf	Nf				Af				A	
Quadrula metanevra	Monkey-face														N	
Quadrula plicata	Blue-point	a	a					N	N		o		A			A
Quadrula pustulata	Warty-back										N					
Quadrula pustulosa	do	NA	A								AN		o			
Quadrula solida																
Quadrula undata	Pig-toe															

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[a] A great many data regarding the hosts of noncommercial species of mussels had been accumulated, but unfortunately most of the records applying to such species were destroyed with the burning of the laboratory in December, 1917.

TABLE 18.—COMMERCIAL MUSSELS AND THEIR HOSTS—Continued.

Mussels.		L. humilis, orange-spotted sunfish.	L. pallidus, bluegill.	L. olivaris, yellow cat.	M. dolomieu, small-mouth black bass.	M. salmoides, large-mouth black bass.	N. maculosus, mud puppy.	P. chrysochloris, river herring.	P. flavescens, yellow perch.	P. annularis, white crappie.	P. sparoides, black crappie.	R. chrysops, striped bass.	S. platorhynchus, sand sturgeon.	S. gyrinus, mad Tom.	S. canadense, sauger.	S. vitreum, walleye.
Scientific name.	Common name.															
Lampsilis anodontoides	Yellow sand-shell	n	o	....	....	na	....	....	o	no	no	a	o	....	o	....
Lampsilis fallaciosa	Slough sand-shell	....	....	o	....	o	....	....	....	n	o	....	n	....	....	....
Lampsilis higginsii	Higgin's eye	....	....	....	....	....	....	....	....	....	....	....	....	....	N	....
Lampsilis ligamentina	Mucket	....	aN	....	N	AN	....	....	AN	NA	A	AN	o	n	A	....
Lampsilis luteola	Fat mucket	....	NA	o	A	A	....	....	AN	A	A	A	o	n	A	NA
Lampsilis recta	Black sand-shell	....	aN	....	....	....	....	....	....	N	....	....	....	....	....	....
Lampsilis ventricosa	Pocketbook	....	A	....	A	A	....	....	A	AN	....	....	....	....	N	....
Obovaria ellipsis	Missouri niggerhead	....	o	....	....	o	....	....	o	o	o	....	NA	....	....	....
Plagiola securis	Butterfly	....	o	....	....	o	....	....	....	o	o	....	....	....	....	....
Quadrula ebenus	Niggerhead	....	o	o	....	o	....	TN	o	o	o	....	o	....	....	....
Quadrula heros	Washboard	....	NA	AN	....	o	n	n	....	NA	A	N	....	Nf	....	....
Quadrula metanevra	Monkey-face	....	on	....	....	o	....	....	....	....	....	....	....	....	N	....
Quadrula plicata	Blue-point	....	a	o	....	AN	....	....	A	Nf AN	A	n	....	....	N	....
Quadrula pustulata	Warty-back	....	....	n	....	....	....	....	....	n	....	....	....	....	....	....
Quadrula pustulosa	do	....	o	an	....	o	....	....	....	on	o	....	n	....	....	....
Quadrula solida		....	N	....	....	....	....	....	....	....	....	....	....	....	....	....
Quadrula undata	Pig-toe	....	....	....	....	....	....	....	....	n	n	....	....	....	....	....

It will be observed that the number of hosts corresponding to a particular species of mussel (as so far determined) varies from one to thirteen. It is of interest to give the number of known hosts for each species of fresh-water mussel, as determined both by observation of natural infections and by the experimental method, and this is done in Table 19.

TABLE 19.—NUMBER OF SPECIES OF FISH KNOWN TO SERVE AS HOSTS FOR CERTAIN SPECIES OF MUSSELS.

Mussels.		Natural infection.	Artificial infection.	Common.	Total.
Scientific name.	Common name.				
Lampsilis anodontoides	Yellow sand-shell	1	3	1	3
Lampsilis fallaciosa	Slough sand-shell	1	1	1	1
Lampsilis higginsii	Higgin's eye	1	0	0	1
Lampsilis ligamentina	Mucket	7	6	4	9
Lampsilis luteola	Fat mucket	3	9	3	9
Lampsilis recta	Black sand-shell	2	0	0	2
Lampsilis ventricosa	Pocketbook	2	5	1	6
Obovaria ellipsis	Missouri niggerhead	1	1	1	1
Plagiola securis	Butterfly	1	1	1	1
Quadrula ebenus	Niggerhead	1	1	1	1
Quadrula heros	Washboard	8	9	4	13
Quadrula metanevra	Monkey-face	2	0	0	2
Quadrula plicata	Blue-point	5	6	2	9
Quadrula pustulata	Warty-back	1	0	0	1
Quadrula pustulosa	do	2	3	2	3
Quadrula solida		1	0	0	1
Quadrula undata	Pig-toe	(?)	0	0	(?)

Table 20 lists the common species of fish showing the number of species of mussels which each fish has been observed to carry as parasites. The greatest number is six, for the bluegill, *Lepomis pallidus*, the white crappie, *Pomoxis annularis*, and the sauger, *Stizostedion canadense*.

TABLE 20.—NUMBER OF SPECIES OF COMMERCIAL MUSSELS KNOWN TO BE CARRIED AS PARASITES BY CERTAIN FISHES.

Fishes.		Natural infection.	Artificial infection.	Common.	Total.
Scientific name.	Common name.				
Ameiurus melas	Bullhead	1	2	1	2
Ameiurus nebulosus	do	0	2	0	2
Anguilla chrysypa	Eel	1	0	0	1
Aplodinotus grunniens	Sheepshead	2	2	2	2
Dorosoma cepedianum	Gizzard shad	1	0	0	1
Esox lucius	Pike	1	0	0	1
Eupomotis gibbosus	Red-ear sunfish	1	0	0	1
Ictalurus punctatus	Spotted cat	2	2	1	3
Lepisosteus osseus	Long-nosed gar	1	1	1	1
Lepisosteus platostomus	Short-nosed gar	1	3	1	3
Lepisosteus tristœchus	Alligator gar	0	1	0	1
Lepomis cyanellus	Blue-spotted sunfish	2	1	0	3
Lepomis euryorus	Sunfish	0	1	0	1
Lepomis humilis	Orange-spotted sunfish	(?)	0	0	(?)
Lepomis pallidus	Bluegill	5	3	2	6
Leptops olivaris	Yellow cat	1	1	1	1
Micropterus dolomieu	Smallmouth black bass	1	2	0	3
Micropterus salmoides	Largemouth black bass	2	4	2	4
Necturus maculosus [a]	Mud puppy	(?)	0	0	(?)
Pomolobus chrysochloris	River herring	1	1	1	1
Perca flavescens	Yellow perch	2	4	2	4
Pomoxis annularis	White crappie	5	5	4	6
Pomoxis sparoides	Black crappie	0	4	0	4
Roccus chrysops	Striped bass	2	2	1	3
Scaphirhynchus platorhynchus	Sand sturgeon	1	1	1	1
Schilbeodes gyrinus	Mad Tom	1	0	0	1
Stizostedion canadense	Sauger	4	2	0	6
Stizostedion vitreum	Wall-eye	1	1	1	1

[a] An amphibian.

It is necessary to point to some significant practical conclusions from the data presented. Since mussels are "choice" as to their hosts, the chances for the successful attachment of glochidia in nature are greatly diminished. The glochidia when discharged from a parent mussel are lost if no fish are at hand to receive them or if the fish that pass are not of one of the very limited number of species which are useful to the glochidia of that particular mussel.

There must necessarily be some definite ecologic relation between the mussel and the fish. The bottom that is inhabited by the hickory-nut mussel must be one that is frequented by the sand sturgeon during the breeding season of that mussel. Again, if one were looking for the river herring, it would be reasonable to expect to find them, during June at least, in places where niggerhead beds are known to exist. It is evident that no species of mussel could exist unless its host were of such habit as to be at the right places at the right times in a sufficient number of cases to permit first, of the infection occurring, and second, of the young dropping where they can survive.

What the factors are that bring mussels and fish into proper association we can not say. In the case of one species of mussel (the pocketbook) at least, it is known that the gravid mussel protrudes from its shell a portion of its mantle as a long brightly marked flap that waves in the water, assuming the appearance of an insect larva or other attractive bait (p. 85). Again we have the sheepshead fish (fresh-water drum) which is known to feed upon small mollusks, mussels, and the sphæriids and univalves that live on mussel beds, and which thus exposes itself to easy infection; sheepshead, indeed, are almost invariably found to be loaded with glochidia. The behavior of the pocketbook is believed to be exceptional, and the sheepshead is one of a very few species of fish known to feed directly upon mussels. It is certain, however, that the fresh-water mussel beds harbor quantities of other small animal life, such as insect larvæ, snails, and worms, and are gardens for the food of fishes (p. 119); in this, probably, lies the principal clue to the association of fish and mussels.

Finally, an economic consideration should be emphasized. The conservation of the fishes is as important to the preservation of the fresh-water mussel resources and the industries dependent upon them as is the propagation and protection of mussels. The disappearance, or the radical diminution in number, of certain species of fish would result in the complete or virtual disappearance of corresponding species of mussel. On the other hand, if the growth of mussels in more or less dense beds produces conditions which are favorable to the growth of fish food, and observations do so indicate, then the disappearance of the fresh-water mussels would result in the diminution of the food supply for fishes, and the conservation of mussels is important for the preservation of our resources in fish.

PARASITISM AND IMMUNITY.

It is worth while to inquire as to the effect of the glochidia upon fish. Are they parasites in the same sense as tapeworms or round worms? Do they sap the vitality of the fish, and are they accordingly to be regarded as in the nature of a disease? While the relation of the glochidium to the fish can not be fully stated in the present stage of investigation, it can be said that the principal effect upon the fish, at first, at least, is the slight laceration of the gills caused by the attachment of the glochidium. The fish quickly heals over this wound to inclose the glochidium and form a small cyst, and after that there is in nearly all cases no evidence of further irritation or of material detriment to the surrounding tissues, except as the cyst and glochidium are sloughed off at the expiration of the proper period.

The fish feels the attachment of the glochidia; it shows that by the flirting movements which are made as infection begins, and it is known that excessive infections of young fish, at least, may cause the gills to become so lacerated and inflamed as to produce the death of the fish (Lefevre and Curtis, 1912, p. 165). The use of small fish is avoided in experiments and operations conducted at Fairport, and as care is taken to avoid excessive infections it can be said that of thousands of fish artificially infected and kept under observation in experimental work at that place there has been no case of death or evidently diminished vitality with evidence to implicate the glochidia as cause.

After the microscopic lesion of the gill is healed over, which usually occurs in the course of a day, the commercial species of mussels generally make little demand upon the fish. No doubt they derive some nourishment from the fish, but this must be very slight, since the young mussels, after spending two or three weeks in undergoing metamorphosis, are found to be of the same size as before they attached to the fish.[a] The demands upon the energies of the fish caused by the glochidia are probably not greater than those arising from a few extra movements.

It has recently been learned that some fish acquire a certain immunity to glochidia, thus being protected against too frequent repetition of infections. Reuling (1919) has found that some of the very large bass, having doubtless experienced some previous natural infections, become immune after one heavy artificial infection, while small bass, without previous infections presumably, require two or three artificial infections before showing immunity. When immunity is acquired, the fish can not be successfully infected with glochidia of any species of mussel. The period of duration of immunity is not known.

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[a] The mussels which grow in size while in parasitism (p. 149) are not commercial species.

An earlier significant discovery had been made by C. B. Wilson (1916, p. 341). His observations and experiments showed that the fish which are most susceptible to glochidia are those which are subject to parasite copepods (fish lice); that there is a definite connection or fellowship of copepods and mussel parasites, so that knowing the species of mussel for which a given species of fish serves as host, one may often predict what species of copepod fish of that species will carry; and finally, that the presence of glochidia on an individual fish renders that fish practically or completely immune to the attacks of the fish lice, and vice versa. These conclusions may be stated in another way: While glochidia and copepods have essentially identical taste in fish hosts, the presence of the one is antagonistic to the other.

These observations indicate that artificial infection of fish with glochidia may have a positively beneficial effect upon the fish in giving it protection against a class of parasites which are pernicious in effect; for copepods are relatively large parasites which sap the vitality of fish and have been known to cause serious mortalities.

The case of the sheepshead or fresh-water drum, *Aplodinotus grunniens*, may be significant. Sheepshead are found to be almost invariably loaded with glochidia upon the gills, carrying infections which would be regarded as highly excessive if caused artificially (Pl. XVI, fig. 1). They are, no doubt, greatly exposed to infection in consequence of the habit of feeding upon molluscs, which they are well fitted to crush with their strong grinding teeth. By carrying successfully glochidia, which they secure while devouring the parent mussel, they are aiding in the propagation of the mussel which may serve them as food. Indeed, the sheepshead unwittingly engages in growing its own food supply. Now, of the fish which have been examined in numbers, the sheepshead is the one species of fish (besides those of the sucker family, which carry neither glochidia nor copepoda) which has never been found to have copepods on the gills. Its immunity from copepods is now easily understood, and it may be presumed that this immunity is worth the cost of almost continually carrying heavy infections of glochidia.

METAMORPHOSIS WITHOUT PARASITISM.

So generally, almost universally indeed, are fresh-water mussels dependent upon fish for the completion of their development, that peculiar interest attaches to the two exceptions which have so far been encountered. Lefevre and Curtis (1911) discovered that glochidia of one species, the squaw-foot, *Strophitus edentulus* Rafinesque, may undergo metamorphosis into the juvenile stage without the aid of the fish (Pl. XVII, fig. 3). In this mussel, as in others, the eggs when deposited in the gills are packed in a formless mucilaginous matrix, but in the course of the development of the glochidia, the matrix becomes changed into the form of many cylindrical cords, in each of which a few glochidia are embedded. There is evidently in this case a special provision for the nourishment of the embryo from materials supplied by the mother, so that metamorphosis of the glochidium is accomplished at the expense of the parent rather than of a fish. Howard (1915) subsequently found that the glochidia of this species could be made to attach to fish and would undergo metamorphosis in the usual way on this fish. He also discovered that the glochidia of another species, a small floater, *Anodonta imbecillis*, developed into the juvenile mussel within the gills of the parent, and that they would not remain attached to fish.

It is significant that there are just a few species of mussels which diverge in two directions from the general rule that fresh-water mussels undergo metamorphosis only in parasitism and without evident growth in size during the process. On the one hand, we have the cases just cited of change of form accomplished without parasitism, and on the other the instances mentioned on page 149 of two or three species in which the larval mussel increases many times in growth while still encysted upon the fish. The tendency manifested by two species is toward independence of fishes or other hosts, while the tendency revealed by a few others is toward a much greater dependence upon fishes. The vast majority of species, including all the mussels having shells of commercial value, occupy the middle ground of limited dependence upon fish; they must live upon the fish, but they require little from them. The hope has been cherished that in time a means would be found of supplying artificially to the glochidia of the common species of useful mussels the food materials and other conditions necessary for the metamorphosis. so that it might become possible to rear mussels without the use of fish. So far, however, failure has marked every attempt to accomplish this purpose.

JUVENILE STAGE.

At the close of the period of parasite life, the young mussel is no longer a glochidia, and while it possesses the rudiments of the principal organs of the adult, it has yet to undergo many changes of structure—or better perhaps, a progressive development in structure—before it fully assumes the adult form and manner of life (Pl. XV, figs. 5 and 6; Pl. XVII, fig. 4). To the intermediate stages, or series of stages, between parasitism and the development of functional sex organs the term juvenile may properly be applied. The siphons or respiratory tubes, the labial palps, outer gills, and sex glands are among the conspicuous features of structure acquired during this stage.

With many and probably most of the common species of mussels, the early juvenile mussel is no larger than the glochidium—in the case of the Lake Pepin mucket slightly less than one one-hundredth inch in length and slightly more than one one-hundredth inch in height. Its thin mussel shell underlies the glochidial shell, and is scarcely visible until after several days of growth. The most conspicuous feature of the young mussel at this time is the foot, which may be protruded from the shell as a relatively long, slender, and active organ of locomotion. The following description applies primarily to the Lake Pepin mucket: The foot is somewhat cleft at the apex to give a bilobed appearance and it is clothed with cilia or minute living paddles, which are in rapid motion while the foot is extended. The foot has also the power of adhesion to surfaces as smooth as glass; by means of it the young mussel can move about rapidly or effect temporary attachments to foreign objects. It is not long before the peculiar characters of the juvenile foot are lost, for during the first month of independent life this organ becomes changed into the characteristic form of the foot of the adult mussel.

At a very early stage a special organ of attachment is formed in some species, especially among the Lampsilinæ (Sterki, 1891, 1891a; Frierson, 1903, 1905; and Lefevre and Curtis, 1912). This is the byssus, a sticky hyaline thread produced by a byssus gland formed in the middle line of the rear portion of the lower side of the foot. In the washboard, *Quadrula heros*, a very few days after leaving the fish there is apparent a tough mucuslike secretion by means of which the juvenile mussel may anchor itself. The byssus may serve to anchor the mussel by attachment to foreign objects, but its function needs to be more definitely ascertained. Juvenile mussels are sometimes captured in considerable numbers, owing to the sticky thread becoming attached or entangled on the crowfoot hooks or lines or on aquatic vegetation drawn into the boat. While such observations suggest the function of keeping the mussel from being carried away by the current, nevertheless the organ is well developed in young Lake Pepin muckets which are observed to bury themselves deeply in the bottom. The byssus is retained a varying length of time in different species and in different individuals of the same species. The byssus has been seen in young muckets, *Lampsilis ligamentina*, late in the second year of free life and rarely in adults of *Plagiola donaciformis*. The species of mussel observed with byssus are listed below.

SPECIES OF MUSSELS THE JUVENILES OF WHICH ARE KNOWN TO HAVE A BYSSUS.

Lampsilis alata, pink heel-splitter.
L. anodontoides, yellow sand-shell.
L. capax, pocketbook.
L. ellipsiformis.
L. fallaciosa, slough sand-shell.
L. gracilis, paper-shell.
L. iris, rainbow-shell.
L. lævissima, paper-shell.
L. ligamentina, mucket.
L. luteola, Lake Pepin mucket.
L. recta, black sand-shell.
L. ventricosa, pocketbook.
Obovaria ellipsis, hickory-nut.
Plagiola donaciformis.
P. elegans, deer-toe.
Quadrula ebenus, niggerhead.
Q. plicata, blue-point.

The shell formed during the first month (more or less) of development possesses certain peculiar characteristics—besides having a relatively low lime content and being transparent, it bears on its surface certain relatively high ridges, knobs, etc. (Pl. XX). The cause or the meaning of these nicely formed ridges is unknown, but the pattern of sculpture of the early juvenile shell is characteristic for the species. Though all the remainder of the shell be perfectly smooth, the "umbonal sculpture," as it is called, can be made out in well preserved adult shells of most species, and their markings are given significance in the classification of mussels.

We need not concern ourselves here with the details of development of the internal organs, except to say that a considerable elaboration of structure must ensue before the mussel is prepared to assume its culminating function—the reproduction of its kind. The first act of breeding marks the close of the juvenile period, and this occurs in the Lake Pepin mucket two years after the beginning of the juvenile stage, or early in the third summer of life counting from the deposition of the egg in the gill of the mother. In some species of mussels, those of small adult size, or those possessing very thin shells, sexual maturity comes at an earlier age, but in most species of mussels it undoubtedly occurs later. (See p. 137.)

The maximum sizes, at various ages, attained by Lake Pepin muckets under observation, are shown in the following table:

TABLE 21.—MAXIMUM SIZE OF YOUNG LAKE PEPIN MUCKETS AT VARIOUS AGES.

Age.	Length.		Age.	Length.	
	Millimeters.	*Inches.*		*Millimeters.*	*Inches.*
Beginning of juvenile stage	0.25	0.01	68 days	13.0	0.51
15 days	.5	.02	5 months	32.3	1.27
38 days	4.2	.17	End of second growing season	58.3	2.30

This species displays perhaps the most rapid growth of any commercial mussel, although it is surpassed in this respect by some of the noncommercial floaters and paper-shells. The maximum size attained in the second year by mussels of several other species reared at the Fairport station is given in Table 22.

TABLE 22.—SIZE AND AGE OF MUSSELS REARED AT FAIRPORT STATION.

Species.	Length.		Approximate age.	Remarks.
	Millimeters.	*Inches.*	*Years.*	
Lampsilis ligamentina, mucket	20.0	0.79	2	Accidentally reared.
Lampsilis anodontoides, yellow sand-shell	41.0	1.62	1¼	Intentionally reared.
Obliquaria reflexa, three-horned warty-back	16.0	.63	2	Accidentally reared.
Plagiola donaciformis	20.0	.79	2	Do.
Quadrula plicata, blue-point	13.5	.53	2	Do.
Quadrula undata, pig-toe	15.8	.63	2	Do.
Obovaria ellipsis, hickory-nut	11.4	.45	2	Do.

Much remains to be learned regarding the habits and habitats of the juvenile mussels of many species. The study is somewhat difficult, because mussels in the juvenile stage are usually hard to find. This is the experience of all collectors, although rich finds of larval mussels are occasionally made in particular locations (Howard, 1914, pp. 34 and 47). In 1914 Shira collected 1,394 juveniles representing 16 species in Lake Pepin, and 92.9 per cent were taken upon sand bottom where there was scattering vegetation. This figure can not, however, be taken as an index of preference for that particular sort of habitat, since 86.2 per cent were taken at one station. Isely (1911, p. 78) made a collection of 32 juveniles comprising 9 species, 6 of which were represented in the Lake Pepin collections, but Isely's specimens were all taken in fairly swift water, 1 to 2 feet deep, and from a bottom of coarse gravel. In rearing young mussels, principally Lake Pepin muckets, in ponds at Fairport, the best success has been attained on prepared bottom of sand; yet when Howard reared Lake Pepin muckets in a crate floating in the river, silt accumulated to a considerable depth, and the juvenile mussels were sometimes found deeply submerged in the soft mud; nevertheless, more than 200 young mussels survived the season in a very small crate, and excellent growth was made.

After the byssus is shed the young mussels often bury themselves in the bottom more deeply than do adults. They are inclined to travel considerably at this stage, but the rate of movement and the distances covered are less than might be thought from observation of the conspicuous and apparently fresh tracks behind the young mussels. It has been found that the tracks will retain the appearance of freshness for several days; hence the trail which one might at first suppose to have been made in a few hours may represent a journey covering a considerable period of time. Clark observed a young mussel which made forward movement every 10 seconds, each movement being followed by a brief rest period. A young hickory-nut mussel was observed to travel 0.1 meter (about 4 inches) in 29 minutes. The rate of travel of sand-shells is much more rapid.

Because of their small size and delicate shell the early juvenile mussels are doubtless the prey of numerous enemies. Turbellarian and chætopod worms are known to devour them. No doubt they are sometimes eaten by fish and aquatic animals, such as are accounted enemies of larger mussels, yet there has been found little evidence of serious depredations upon young mussels by such animals. Perhaps the most serious natural mortality among juvenile mussels occurs from falling upon unfavorable bottoms or from the effects of currents, especially in times of flood, which may draw the relatively helpless mussels into environments in which they have small chance for survival. It may be expected, too, that the repeated dragging of crowfoot bars over favorable mussel bottoms works damage to juveniles both by injuries directly inflicted and by pulling them from the bottom and exposing them to the action of currents from which they had previously found protection.

ARTIFICIAL PROPAGATION.

PRINCIPLE OF OPERATION.

As the previous account of the life history of fresh-water mussels has shown, the mussel not only deposits great numbers of eggs but nurtures them in brood pouches within the protection of her shell. There is not, as in fish, a great wastage of eggs and larvæ in the very earliest stage of development. There exists, therefore, no necessity for artificial aid to effect fertilization; that is, to bring the male and female reproductive elements together. Nature's own provisions have adequately provided for the bringing of enormous numbers of each generation of offspring to the glochidium stage. It is after this stage is attained that the greatest mortality occurs; the great abundance of glochidia produced by each female is, indeed, evidence that enormous losses are to occur subsequently, and observation indicates that the critical stages are, first, when the glochidia are liberated from the parent to await a host, and, second, when the juvenile mussels are dropped from the fish that serves as host.

The artificial propagation of mussels as now practiced aims to carry the young mussels through the first great crisis. Its object is to insure to a large number of glochidia the opportunity to effect attachment to a suitable fish. Under present conditions the operations can be conducted extensively and economically only in the field. The procedure in brief is to take fish in the immediate vicinity of the places to be stocked, infect them with glochidia of the desired species of mussels, and liberate them immediately. Artificial propagation, then, as applied to fresh-water mussels, is a very different sort of operation from that employed in the propagation of fish, although it is no less directly adapted to the conditions and needs of the objects to be propagated.

METHODS.

In each field the operations are conducted under the immediate direction of a qualified person who may be either a permanent or temporary employee of the Bureau working under the Fairport station. The fishing crew is comprised of three or four local fishermen, or laborers, temporarily employed.

The equipment for seining and handling the fish consists of a motor boat, one or two flat-bottomed rowboats, seines or other nets, including small dip nets, tanks, buckets, etc. The motor boat is used to cover the various fishing grounds as rapidly as possible to distribute the infected fishes, and to move the outfit from place to place as it becomes advisable or necessary to extend the field of operations. The rowboat is employed in the actual work of seining and handling the fish. If the fish are taken in very large numbers it is convenient to have one or two tanks, similar to the ordinary 4-foot galvanized stock tanks and equipped with handles. Under ordinary conditions, tubs serve very well, especially if the fish have to be transported by hand for some distance, as is the case when the fish are taken in rescue work from land-locked ponds or lakes. At times, when the field of operations is at some distance from a place where living and sleeping accommodations can be secured, a camping outfit, or a house boat, is used for quartering the crew. The head of the party must be provided with a dissecting microscope, a magnifying hand lens, and simple dissecting instruments.

Before an infection can be made, it is first necessary to obtain a supply of glochidia of the desired species of mussels. In localities where commercial shelling is actively practiced this can be done by visiting the shellers' boats and examining the catch for freshly-taken gravid mussels. If it is desired to use the glochidia at once, the brood pouches are immediately cut from the females and placed in water; but if it is desired to use them over a period of several days, the gravid shells are purchased and the glochidia removed as needed. In locations where shells are scarce, or where little or no commercial shelling is done, it is sometimes necessary to hire a sheller to procure the mussels.

The fish are next sought by means of seines or nets, and when secured are sorted and transferred to the tanks or tubs; the fish that are not required for purposes of mussel propagation are immediately liberated in suitable waters. When the containers are comfortably filled with fish, overcrowding being avoided, the brood pouches of one or more mussels, as necessary, are cut out and opened with scissors or scalpel and the glochidia are teased out in a small pail or other container from which they are poured into the tanks with the fish. Figures 1 to 4, Plate XVIII, show the seining and infection operations in the field.

The experienced operator can usually tell at a glance whether or not the glochidia are sufficiently ripe for infection. If they freely separate when removed from the brood pouches and placed in a dish of water, it is usually a sign that a sufficient degree of ripeness has been obtained. If, however, they adhere in a conglutinate mass and can be separated only with difficulty, it is certain indication that they are unsuitable for infection; examination with a hand lens in such case will show also that the glochidia are still inclosed in the egg membrane, thus revealing their immaturity. If the glochidia are fully developed, one can readily determine if they are alive and active by dropping a few particles of salt or a couple of drops of fish blood into a small dish containing some of the glochidia. It is a sign of maturity and vitality if the valves begin to snap together as the salt or blood diffuses through the water.

After being removed from the brood pouches the life of the glochidia is usually rather short, but it is possible to keep them alive a day or two if the water in which they are retained is changed at frequent intervals and not permitted to become too warm.

The operator is guided by his experience as to the quantity of glochidia to be placed with a given lot of fish and as to the length of the infection period. The water may be stirred from time to time in order to keep the glochidia in somewhat even suspension, but in most cases the movements of the fish themselves insure a circulation of the water and a general distribution of the glochidia. At intervals individual fish are taken by hand or small dip net, and the gills examined with a lens; when, in the opinion of the operator, a sufficient degree of infection has occurred, the fish are placed at once in open waters, or transferred to other containers for conveyance to a place suitable for their liberation. The rapidity with which infection takes place depends upon a variety of conditions, such as temperatures of water, kind and size of fish, and activity of glochidia. Ordinarily a period of from 5 to 25 minutes is sufficient to insure an optimum infection. The infection time is usually shorter in warm water than in cold. As basis for approximate computation of the number of glochidia planted, several average-sized specimens of each species of fish infected are killed and the gills removed for subsequent counts of the glochidia attached. The counting is done by the foreman with the aid of a microscope and usually in the evening after the close of the field operations of the day. The number of glochidia per fish of each species having been determined by the count of representative examples, and the numbers of fish of the species being known, the entire number of glochidia planted on a given lot of fish is easily computed. The data in detail are promptly recorded on form cards provided for the purpose. The count of total glochidia planted is of course only approximate, but the method of count and computation described is as accurate as the conditions of operation permit, and it is as precise as the methods of count generally practiced in fish-cultural operations. In the long run, the actual errors on one side and the other must approximately balance.

That degree of infection which employs the fish to best advantage in mussel propagation, without doing appreciable injury to the host, is termed the "optimum infection." It varies with the species of mussel and with the kind and the size of the fish. Table 23 gives illustrative instances.

TABLE 23.—OPTIMUM INFECTION FOR CERTAIN SPECIES OF MUSSEL ON SEVERAL SPECIES OF FISH.

Species of mussel.		Fish host.		Number of glochidia on fish.
Scientific name.	Common name.	Species.	Size in inches.	
Lampsilis luteola	Lake Pepin mucket	Black bass	8	2,000
Do	do	White bass	8	2,000
Do	do	Wall-eyed pike	8	2,500
Do	do	Bluegill	5	500
Do	do	Crappie	5	400
Do	do	Yellow perch	6	1,500
Lampsilis anodontoides	Yellow sand-shell	Gar	16	2,000
Lampsilis ligamentina	Mucket	Black bass	8	2,000
Lampsilis pustulosa	Pimple-back	Channel catfish	14	1,200

Incidental to the field work in mussel propagation, valuable results are frequently gained in the reclamation of fish from the overflowed lands bordering the various rivers. All fishes rescued in connection with propagation work, whether suitable or unsuitable for infection, are liberated in the open waters, and under such circumstances the value of the fish thus saved in large measure recompenses for the cost of the mussel propagation work.

The operations of mussel propagation as just described serve to carry the young mussels through the most critical stage of the life history—to give to thousands the

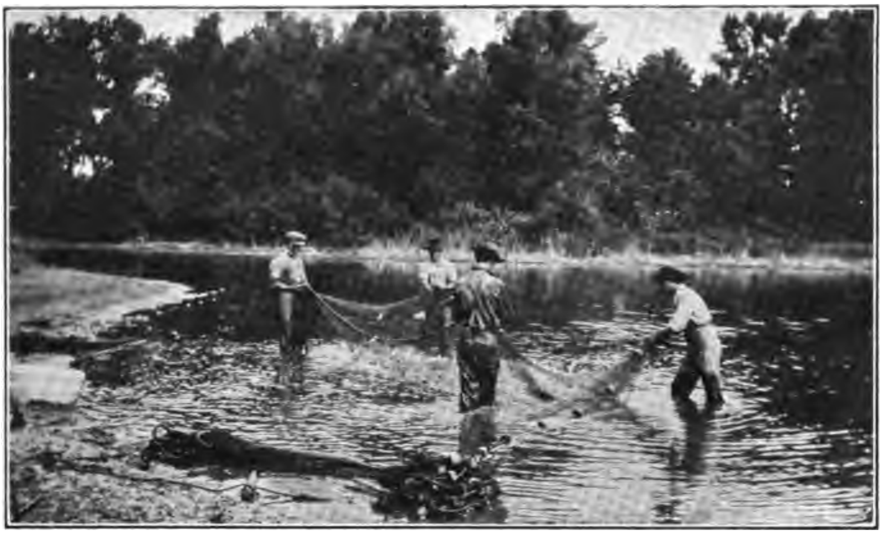


FIG. 1.—Seining fish from overflow water for infection with glochidia of mussels.

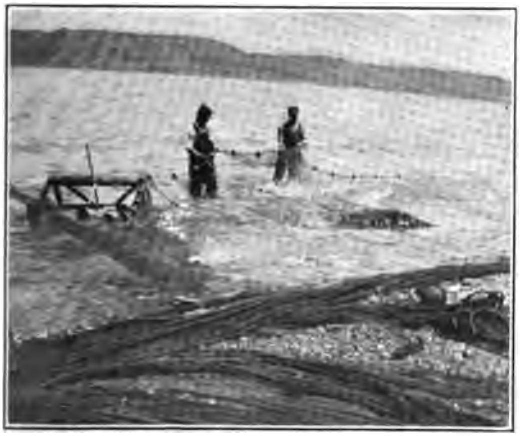


FIG. 2.—Seining fish in Lake Pepin for mussel propagation.

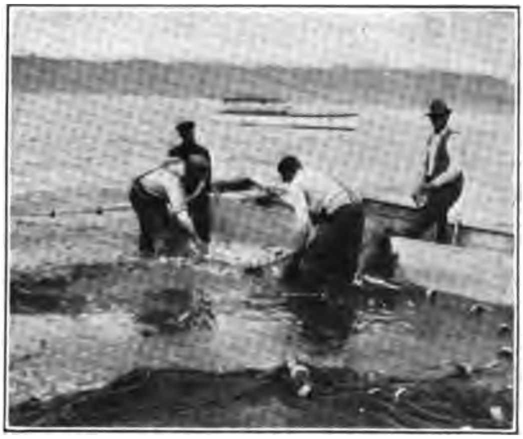


FIG. 3.—Transferring fish to infection tank. Foreman in boat is pouring the glochidia from a can into the tank.

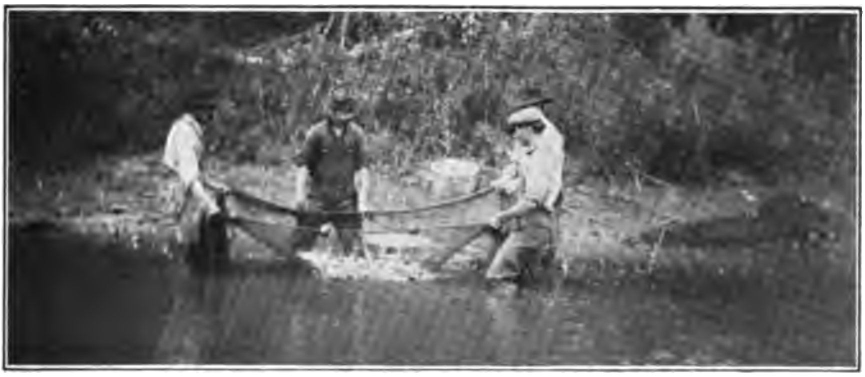


FIG. 4.—Sorting the fish for infection with glochidia.

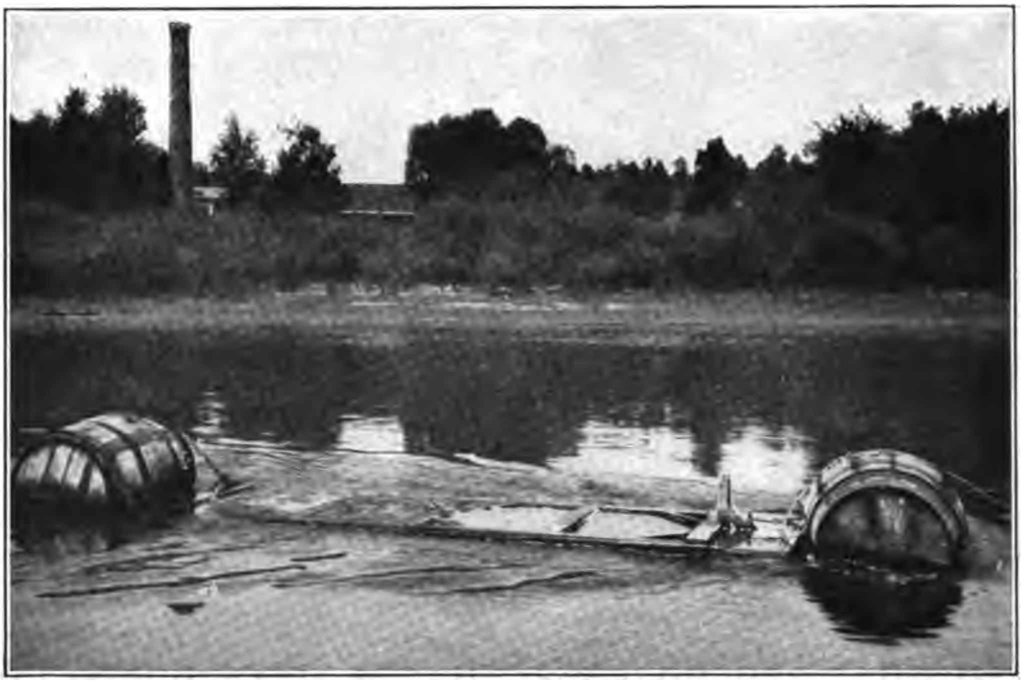


FIG. 1.—A floating crate containing four baskets in which fish infected with glochidia were placed and young mussels reared. (Compare Pl. V, fig. 3.)

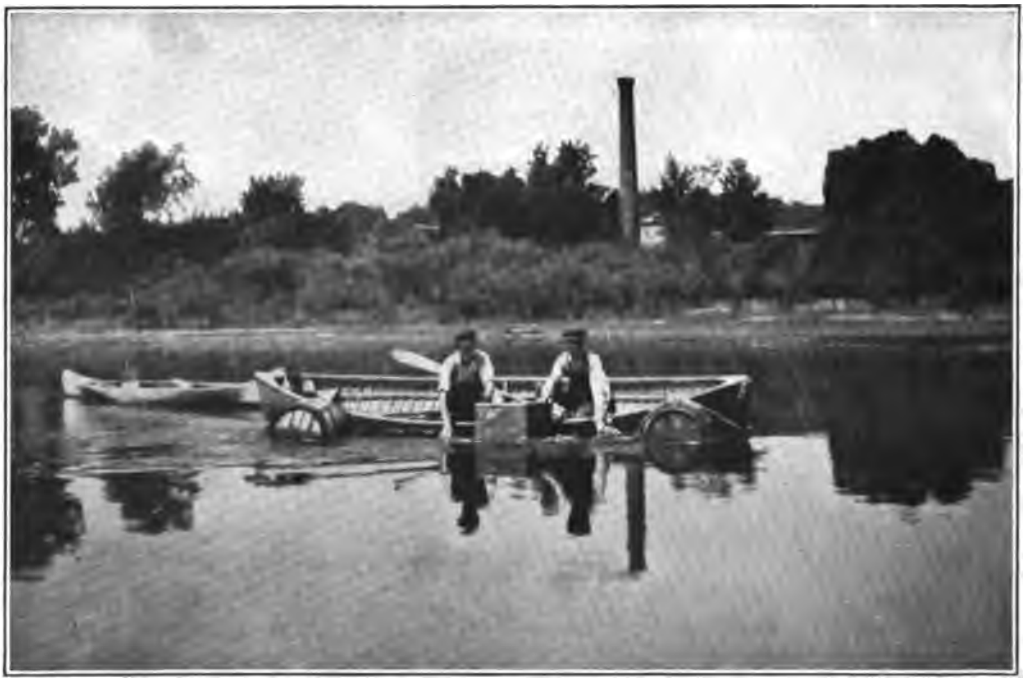


FIG. 2.—Lifting one of the baskets from the crate for examination and cleaning.

chance of life that would ordinarily fall only to dozens. As previously pointed out (p. 151), an extensive series of observations of fish reveals the fact that but few are naturally infected with mussels and these usually in slight degree. The chance that a large proportion of the glochidia discharged by any mussel will become attached to a proper host is slight, and it is only because nature is prodigal in the production of glochidia that the various species of mussels can maintain their numbers under natural conditions. With the disturbance of natural conditions by the active pursuit of a commercial shell fishery, nature's fair balance is destroyed, and some compensatory artificial aid to the propagation of mussels is rendered necessary.

It is not presumed that all the vicissitudes of mussel life are removed by the bringing together of fish and mussel. Nature undoubtedly exacts heavy tolls at other stages. Many of the young mussels on being liberated from the fish will fall in unfavorable environments and meet an early death, while those that survive the earliest stage of independent life may still be subjected to numerous enemies throughout the juvenile period at least. Nevertheless, glochidia of certain species can be planted in such large numbers and at such slight cost that, after making due allowance for an extraordinary subsequent loss, substantial returns can be expected. That such results do obtain is indicated both by experiments to be later described (p. 166) and by common experience

MUSSEL CULTURE.

The rearing of young mussels in tanks, in ponds, or (if under conditions of control) in the river, may properly be termed "mussel culture," as distinguished from "mussel propagation," which, as we have seen, consists in bringing about the attachment of glochidia to fish and liberating the fish in public waters. For several years experiments in mussel culture have been carried on by the Bureau of Fisheries at Fairport and elsewhere, with a view both to securing information regarding the life history of mussels and to testing experimentally the possibilities of culture as a public measure of conservation or as a field for private enterprise. At first little success attended these efforts. It was found that the mussels could readily be carried through the parasitic stage, but that soon after leaving the fish hosts they perished. Apparently there was something inimical to the young mussels in the artificial conditions of aquaria, tanks, or ponds, although these might be supplied with running water derived from the natural habitat of mussels.

The first reported rearing of mussels under control was accomplished with the Lake Pepin mucket in a crate floating in the Mississippi River (Howard, 1915). Experiments initiated by the senior author in the ponds at Fairport, Iowa, about the same time were also successful with the same species. Subsequently broods of the Lake Pepin mucket have been reared from year to year by various methods. Less consistent results have been obtained with the following river mussels: The pocketbook, *Lampsilis ventricosa*, the pimple-back, *Quadrula pustulosa*, and until recently the yellow sand-shell, *Lampsilis anodontoides*, and the mucket, *Lampsilis ligamentina*. Apparently the conditions required for rearing the Lake Pepin mucket are less difficult to meet under control than is the case with the other species mentioned. The reason is, doubtless, that *Lampsilis luteola*, being a lake-dwelling species as well as an inhabitant of rivers, is adapted to more varied conditions.

The methods employed in rearing mussels may be designated as follows: (1) The floating crate with closed bottom (chiefly used in rivers); (2) the floating crate with open bottom (chiefly used in ponds); (3) the bottom crate; (4) pen with wooden or box bottom; (5) concrete ponds; (6) earth ponds; (7) troughs of sheet metal, wood, or concrete tanks, and aquaria.

(1) The floating crate with closed bottom was devised to meet the special conditions of a large river where the level is subject to considerable change, where excessive turbidity frequently prevails, and where there is a decided current. To prevent the washing away of the microscopic mussels, while permitting the passage of water and food through the crate, the crates are constructed of fine-meshed (100 mesh to the inch) wire cloth on a wooden frame. The form of the crates and the manner of using them may be understood from the illustrations (Pl. XIX, figs. 1 and 2). They are described in more detail in a forthcoming paper by A. D. Howard. A plant of young mussels is obtained by placing infected fish in the crate and removing them after they are freed of the mussels. The results with the floating crate have been quite satisfactory with the Lake Pepin mucket, and a few yellow sand-shells have also been obtained in them. Other river mussels have failed to develop beyond early stages. Good results with river mussels would be expected, but it is found that even with the crate floating in the river, the conditions within it are not those of the natural habitat of the mussel on the clean current-swept bottom of the river. No one has yet devised a container to employ under such conditions that would fully answer the requirements.

(2) The floating crate with open bottom has been used in artificial earth ponds. The bottom is actually closed to fish, though open to juvenile mussels, since it is made of coarse-mesh wire cloth (1½-inch mesh). The infected fish are kept inclosed until freed of glochidia, which fall through the wire to the bottom of the pond. To obtain the mussels when developed, the water is temporarily drawn from the pond. Good results have been obtained with the Lake Pepin mucket only.

(3) The bottom crate has been used in studies of growth of larger mussels, by Lefevre and Curtis (1912, p. 180), Coker, and others, and in experiments in pearl culture by Herrick (Coker, 1913). It has recently been adapted for the purpose of retaining infected fish and securing plants of early postparasitic stages of mussels. The crate rests on the bottom of the pond. It may have either a solid bottom or one of screen wire which, of course, sinks a little way into the mud covering the bottom of the pond.

(4) The pen of galvanized netting with wooden floor is adapted to quiet water without current. The pen, having walls of wire cloth that extend from the bottom to a safe distance above the surface of the water, allows the fish to seek their own range of depth and permits the mussels that fall from the fish to remain close to the bottom of the pond or lake, as is natural for them. The mussels are collected by raising the wooden bottom at the end of the growing season. Excellent results have been obtained in Lake Pepin with the Lake Pepin mucket. In the most successful experiment more than 11,000 living young were secured in one crop in a pen 12 feet square. These were liberated from 79 fish which had been artificially infected (Corwin, 1920).

(5) Concrete ponds having vertical sides have been planted in the usual way and the fish removed with a seine after the mussels have been shed. Some 50 examples of a river-inhabiting species, the pimple-back, *Quadrula pustulosa*, were reared to the age of 4 years in one experiment, but other trials with this species have failed. The usual consistent results have been secured with the Lake Pepin mucket.

(6) Earth ponds with devices for control of depth and water supply have been stocked with mussels by introducing infected fish. As a rule the fish are not removed

until the end of the season when the pond is drawn. The Lake Pepin mucket in considerable numbers have been reared in earth ponds. A few pocketbook mussels, *L. ventricosa*, were obtained after a recorded plant in a pond of modified type, having earth bottom but wooden sides. Mussels of several other species have been found in ponds from accidental plantings. The sporadic occurrences of young mussels in the first ponds and in the reservoir constructed at the Biological Station at Fairport, Iowa, are of interest as showing how, through parasitism upon fish, many species of mussel will quickly invade new waters. It is significant that none of the species which have introduced themselves abundantly into these ponds are commercially valuable. Apparently the commercially useless mussels are more easily and abundantly distributed by natural means than the useful ones. A list of the species noted, with additional data, is comprised in the following table (cf. Pl. XX):

TABLE 24.—MUSSELS RECORDED FROM PONDS AT THE FAIRPORT STATION.

Scientific name.	Common name.	Number or frequency.	Length in millimeters.
Anodonta corpulenta Cooper	Floater	Abundant	60-90
Anodonta suborbiculata Say [a]	Paper-shell	3	67.4
Anodonta imbecillis Say	do	Abundant	2-48
Arcidens confragosus Say [a]	Rock pocketbook	7	39-49
Lampsilis ligamentina Lam	Mucket	7	6-20
Lampsilis (Proptera) alata Say	Pink heel-splitter	2	69.5
Lampsilis (Proptera) capax Green	Pocketbook	2	49.5
Lampsilis (Proptera) lævissima Lea	Paper-shell	Abundant	27-90
Lampsilis subrostrata Say [a]		do	8.48
Lampsilis gracilis Barnes	Paper-shell	do	9.1-71
Lampsilis parva Barnes [a]		do	5.7-27
Obliquaria reflexa Rafinesque	Three-horned warty-back	1	16
Plagiola donaciformis Lea	Deer-toe	Abundant	2.6-20
Quadrula plicata Say	Blue-point	1	13.5
Quadrula undata Barnes	Pig-toe	1	15.8
Strophitus edentulus Say [a]	Squaw-foot	1	62.1
Symphynota complanata Barnes	White heel-splitter	26	64-91
Obovaria ellipsis Lea	Hickory-nut	1	11.4

[a] Uncommon in the river.

(7) Experiments have also been made with various containers of small dimensions which are usually supplied with running water. Such are the glass aquarium and the tank or trough which may be made of wood, concrete, or sheet metal. Of these the one most used for experimental rearing of mussels at Fairport, Iowa, has been the trough of sheet metal painted with asphaltum. A special arrangement for water supply is employed. The water is not taken directly from the main reservoir, but is drawn from the surface of a pond containing vegetation; in some cases it is also strained through cloth. In this way water is obtained that is very clear and probably free to a large extent from such small animals of the bottom as would prey upon the young mussels. The Lake Pepin mucket, the river mucket, and the yellow sand-shell have been reared through the first year in such troughs. The experiments are of such importance as to merit detailed description. The following account is based upon a report of F. H. Reuling, who first assisted in the experiments and later was charged with their conduct. (See also Reuling, 1919.)

The experiments were conducted in a series of eight galvanized iron troughs, placed at a sufficiently low level to receive a gravity supply of water from pond 1D. This pond was supplied by gravity from the reservoir which received its supply direct from the Mississippi River through the pumping plant. The water in pond 1D remained comparatively clear throughout the season, and this was one of the primary considerations in locating the troughs. The troughs were 12 feet long, 1 foot wide, and 8 inches deep, painted with asphaltum, and each had its independent inflow from a common screened supply pipe in the pond. The bottom of each trough was covered with fine sand to a depth of about one-half inch.

Records were kept of the progress of the larval mussels through the process of development, and when they had reached that stage when they were ready to drop from the fish, counts on the fish gave a close approximation of the number dropped in the trough.

The results of the experiments the first season were quite meager, as only 7 young of the Lake Pepin mucket, *Lampsilis luteola*, varying from 6 mm. to 17.8 mm. in length, and 4 of the mucket, *L. ligamentina*, with an average length of 2.6 mm., were reared. However, in case of the mucket the results were very encouraging, as it marked the first instance of juveniles of this species being artificially reared to this size.

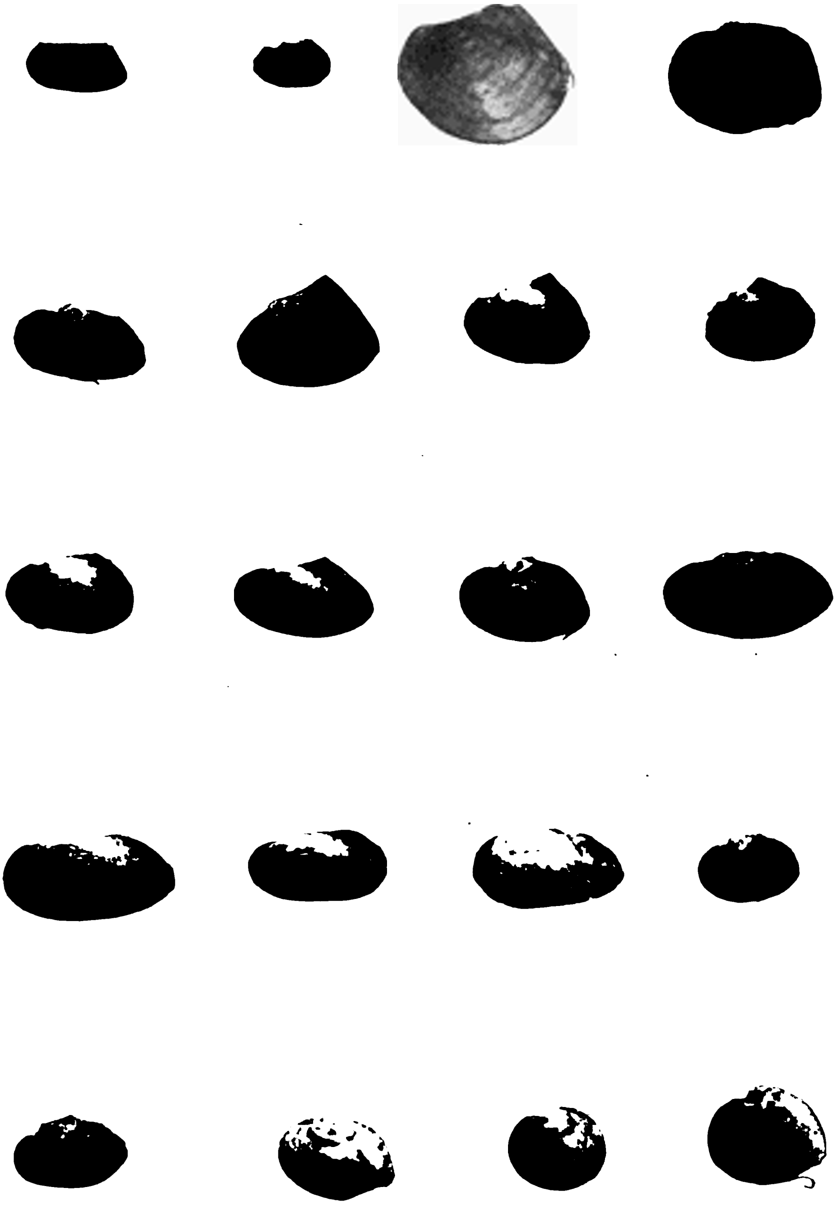
During the season of 1918 greater results were obtained with the Lake Pepin mucket, the young mussels being successfully reared in four troughs. In one trough a count of 746 was obtained. The experiments with *ligamentina* yielded negative results, though a lack of glochidia for infection greatly handicapped the work with this species.

The results in 1919 were still more gratifying. Young Lake Pepin muckets were obtained in each of five troughs planted with this species. In one trough 2,008 were counted at the end of the season, these little mussels varying in length from 9 mm. to 17.5 mm., the growth comparing very favorably with that made by the young of this species in their natural habitat. In a trough devoted to the river mucket, *L. ligamentina*, a total of 565 were reared. These little mussels varied in length from 5 mm. to 8.5 mm. In a trough planted with the yellow sand-shell a count of 2,006 was obtained at the end of the season, the young mussels varying in length from 5.5 mm. to 12 mm. The result of this experiment is highly interesting, in that it is the first record of the artificial rearing of this very valuable species in any quantity.

The 746 young *luteola* reared during the summer of 1918 were carried over the winter in a shallow crate bottom 5 feet square and 8 inches deep, submerged in one of the earth ponds. During the summer of 1919 an inventory of the crate bottom gave a count of 238 young mussels, a survival percentage of about 32 per cent.

The method of artificial rearing of young mussels, as detailed above, denotes a distinct departure from the methods previously used and gives the operator complete control of conditions throughout. The results of the experiments have been such as to justify the employment of the method on a much larger scale in future, and plans are under way for materially increasing the facilities and equipment. Certain phases of the work need further study and amplification. Additional information on the possible enemies of the young mussels in the troughs is needed; a study of their food should be made; it should be learned if artificial feeding is practicable; and further experiments should be made to determine the most favorable bottom material for the troughs, whether fine sand alone, or sand with a slight admixture of silt, etc. The present indications are that fine sand is the most desirable bottom material.

In summary of the topic of the culture of fresh-water mussels, it may be stated that the results of many experiments conducted under diverse conditions demonstrate that the valuable Lake Pepin mucket can be reared in quantities, under conditions of control. Sufficient success has been attained with other species to warrant confidence that, with them also, methods of securing constant results will be found.



Juveniles of 20 species of mussels found in the artificial ponds at the U. S. Fisheries Biological Station within two years from the time of construction of the ponds. Reading from left to right these are:

Top row: *Anodonta imbecillis*, *Anodonta corpulenta*, *Anodonta suborbiculata*, *Arcidens confragosus*.
Second row: *Strophitus edentulus*, *Symphynota complanata*, *Lampsilis alata*, *Lampsilis laevissima*.
Third row: *Lampsilis capax*, *Lampsilis gracilis*, *Lampsilis ventricosa*, *Lampsilis luteola*.
Fourth row: *Lampsilis subrostrata*, *Lampsilis parva*, *Lampsilis ligamentina*, *Obovaria ellipsis*.
Fifth row: *Plagiola donaciformis*, *Obliquaria reflexa*, *Quadrula plicata*, *Quadrula undata*.

All reproduced natural size excepting the two right-hand figures in top row which are reduced one-half. (Photographed by J. B. Southall.)

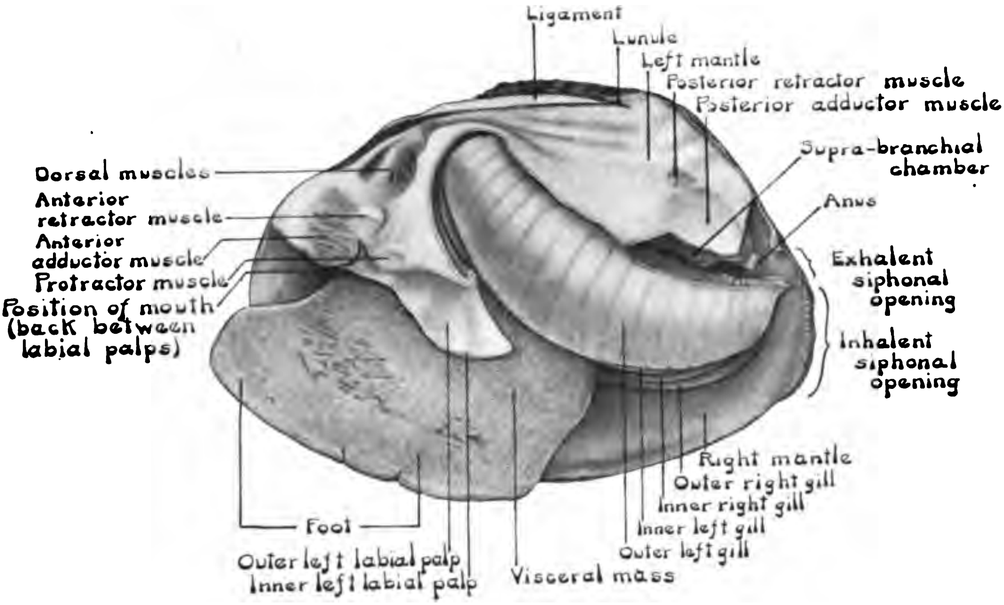


FIG. 1.—The structure of a fresh-water mussel. (Based upon drawing of white heel-splitter, *Symphynota complanata*, from Lefevre and Curtis, 1912.)

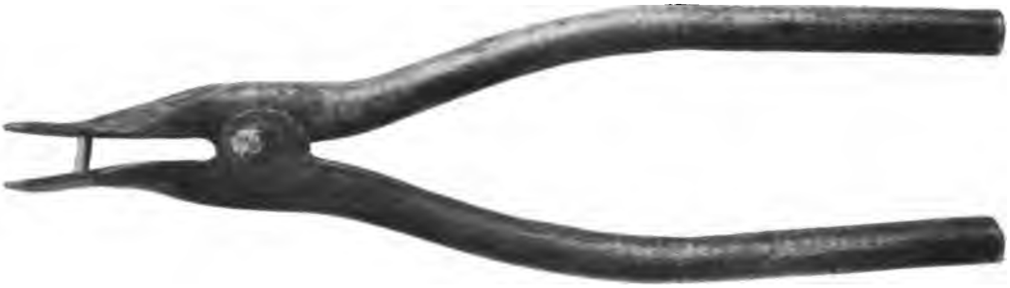


FIG. 2.—A tool which, if employed with care, may be used for partially opening living mussels for examination of conditions within the shell.

PART 3. STRUCTURE OF FRESH-WATER MUSSELS.

INTRODUCTION.

A general description of the structure of fresh-water mussels may assist those without special knowledge of the anatomy of mussels to follow intelligently the account of the natural history, propagation, and development which it has been the primary purpose of this report to give. It may also serve as a helpful introduction to persons with limited technical knowledge who wish to make original observations or experiments concerning the habits and growth of mussels. It has been the special purpose of the authors to point out the more conspicuous gaps in our knowledge of the behavior of mussels and their relations to the environment. Many of these gaps can readily be bridged by any who will take the trouble to observe painstakingly and repeatedly the conditions under which fresh-water mussels live in the streams, lakes, or ponds in one's own neighborhood. The species subjected to observation or experiment should of course be definitely known, but identifications of species can always be obtained of Government agencies or from independent specialists in the study of mollusks.

In most localities some species of mussels are easily obtainable and observable in nature or in aquaria. In rivers of the Atlantic States, generally, the common mussel is the *Unio complanatus*. The more familiar forms in lakes and alongshore in streams of the Mississippi Valley and the Great Lakes drainage are the fat mucket *Lampsilis luteola*,[a] and some of the floaters of the genus Anodonta. Closely related to the fat mucket is the mucket, *Lampsilis ligamentina*, which is common in the Mississippi and its tributaries as well as in many streams discharging into the Great Lakes. As a representative type in the simplicity of its form and of the sculpture and markings of its shell, the mucket serves as the basis of the following general description, except as explicit qualifications are made. With more or less modification, the account may be applied to whatever species is most readily available. The functions of the organs described will generally be briefly indicated.

Let it be understood first that a living mussel is commonly partly embedded in the bottom, with the forward end directed obliquely downward and the rear end upward. The "mouth" as understood by fishermen is in reality the double siphonal opening in the hinder part of the mussel; the true mouth, through which food is taken into the body, is a very small and scarcely discernible opening in the part of the soft body which is farthest away from the exposed end of the mussel.

The fresh-water mussels differ markedly in structure from the oyster or the pearl oysters which pertain to a different order of lamellibranchs. They are likewise far removed from the sea mussels, which lie in a third order. Their nearer relatives are the sea clams and the small Cyrenians of the rivers; the sea clams and the little clams (Cyrenians) of the rivers are more closely allied to each other than to fresh-water mussels. The pearly fresh-water mussels or Naiades comprise two great families, the Unionidæ, with which the present paper is concerned, and the Mutelidæ of South America and Africa. The Mutelidæ differ from the Unionidæ in some particulars of structure, especially in the form of teeth on the shell and in the form of larva, which is a *lasidium*, instead of a glochidium such as has been described above.

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[a] The best commercial type of the mussels of this species is also known as the "Lake Pepin mucket."

THE SHELL.

The shell is composed of two parts very similar in exterior aspect, but generally differing from each other in interior form. Each portion is called a valve, and the two valves are hinged together.

EXTERNAL FEATURES.

In form the shell is roughly elliptical, evenly rounded in front, but more or less angular behind. The lower or ventral margin is generally evenly rounded, but may be arched inward just behind the middle, especially in shells of females. The dorsal or hinge margin is rather straight except for the rounded prominence on each valve just in front of the middle of the back; this knob, or arched portion of each valve, is called the umbo. Where the umbones of opposite valves approximate each other they are more or less elevated above the surrounding shell surface to form the beaks. The beaks in many species, though not in the mucket, are beautifully sculptured with coarse or fine ridges in the form of single or double loops. With the river mucket, beak sculpture is entirely wanting, while it can be seen clearly in *Symphynota complanata* (Pl. XX, 2d row, 2d fig.). Almost every species, if good specimens are available, show some form of beak sculpture;[a] commonly, however, in older specimens the beaks are so much eroded that the ridges are hardly, if at all, apparent.

In some streams scarcely a single example can be found with the beaks preserved; in other waters erosion occurs less commonly and the beak markings can be observed even in some of the large examples.

In some cases the resting periods of winter have left distinct marks by color or otherwise on the shell, so that rings or zones corresponding to the growth of each year are recognizable. The rings of annual growth are not, however, generally recognizable on shells having a dark-colored exterior surface. It is also observed that such rings may result from other causes than the interruption of growth by the severity of winter. (See p. 132.)

A conspicuous feature of the shell is the prominent ridge, which extends from the beaks backward and downward to the posterior ventral angle of the shell. A somewhat similar ridge characterizes almost every species of mussels.

The exterior color of the shell is a most variable character. Generally speaking, the body color is a greenish straw, relieved by narrow green rays, very narrow on the beaks and widening out toward the lower margin. These rays are a nearly constant character in the mucket, but vary in number, in width, in brightness of color, and in being continuous or interrupted. The periostracum, or horny covering, of shells growing in clear streams is generally much more brightly rayed than that of those in turbid ones. Young shells are more brightly rayed than old, the rays generally fading somewhat or wholly disappearing with age. In different localities, and even in the same bed, the colors are various, the shells may be nearly uniformly straw-colored or largely green; again, a red or rusty-brown color may predominate. The red color without is commonly associated with a pink nacre within. The shell may be smooth and glossy or roughened by fine lines; a silky appearance may be caused by innumerable fine laminæ or folds projecting out from the surface of the periostracum. The silky surface is characteristic of some species, as the hickory-nut, *Obovaria ellipsis*.

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[a] The beak sculpture of young specimens is a very important diagnostic character or means of distinguishing species which may closely resemble each other in general form. Compare the yellow and the slough sand-shells, *Lampsilis anodontoides* and *Lampsilis fallaciosa*, or the pocketbooks, *Lampsilis ventricosa* and *Lampsilis* (*Proptera*) *capax*, which are occasionally distinguished by this feature alone. The beak is, of course, the beginning of the shell—the oldest portion.

Looking now at the top or hinge of the shell there is seen just back of the beaks a long, narrow, tough, leathery, elastic band, the ligament, an important part of the hinge mechanism. Just in front of the beak is a small region between the shell valves, which is occupied by a similar horny material. This is called the anterior lunule, but in the mucket it is scarcely developed, being about one-half inch long and very narrow in a specimen of 3 inches total length. A posterior lunule may be found just back of the ligament. The compressed form of the shell is noticeable in this view. Roughly speaking, the thickness of a mucket from side to side is about one-third of the length, while the width—or height, more correctly—is about two-thirds of the length.

INTERNAL FEATURES.

The interior surface of the shell is smooth, white, and lustrous, and usually somewhat iridescent in the extreme posterior portion. In color it is white or pinkish in the mucket, but in other species it may be salmon or purple. Often the proper color is obscured by yellow, greenish, rusty, or salmon-colored stains, resulting from disease, injury, or inclusion of mud in the nacre. The body of the shell is mainly calcareous, being composed chiefly of a compound of calcium of somewhat the same chemical composition as marble or limestone, but differing in physical structure from either. An account of the structure of shell is given in another place (p. 129).

The conspicuous features of the interior aspect of the shell are the general concavity of each valve; the deeper beak cavities; the dorsal margin roughened by ridges or protuberances known as the "teeth;" two rounded, impressed, and roughened surfaces, one near each end, the adductor muscle cicatrices; and a curved impressed line parallel to the margin of the shell, extending between the two scars just mentioned. This last is the pallial line and marks the attachment of certain muscles of the mantle.

The two valves, it is noted, are practically identical except for the teeth, which instead of being equal in the two valves, correspond to each other in such a way that the teeth of one valve fit into the spaces between the teeth of the opposite valve. The two valves are thereby interlocked so that they can not slide over each other. Heavier teeth characterize the mussels that are adapted to live in strong currents, while weak teeth or the total lack of them mark the species that must live in quiet waters. The teeth in each valve are of two forms; at the anterior or front end are the stout, rough, and somewhat conical cardinal or pseudocardinal teeth; while behind these, and more or less separated from them, are long, narrow, bladelike ridges, the lateral teeth. On the right valve there is one lateral tooth which exactly fits into the deep narrow furrow between the two slenderer lateral teeth of the left valve. The two valves are practically exact mirror images of each other except for the teeth; accordingly, in species such as the

Anodontas, which are without teeth, the bilateral symmetry is complete. In some marine bivalves the two shells are essentially different, as in the oyster, where one is concave while the other is flattened and smaller.

The ligament is composed of two parts; the dark outer layer is inelastic and continuous with the periostracum of the shell; while the inner part, comprising the bulk of the ligament, is elastic and bears somewhat inappropriately the name of cartilage. The elastic cartilage is confined between the inelastic layer above and the firm hinge of the shell below. It is compressed when the shell is closed. The natural or relaxed condition of the shell is, therefore, open; that is to say, with the valves separated below by about one-half inch. Consequently, the shell is kept closed in life only by an exertion on the part of the animal. This is accomplished by means of two stout bands of muscle fibers, constituting the anterior and posterior adductor muscles, which extend from one valve to the other near each end of the shell. These are firmly attached to the shell at each end, the places of attachment being the conspicuous rounded impressions previously noticed.

The hinge mechanism is completed by the lunule previously referred to. This is a thin horny covering occupying the space between the valves in front of the beak. Unlike the ligament behind, it is stretched when the shell is open. The lunule doubtless has no especial significance except to serve as a protective covering and to make a firm union of the two valves.

Besides the two adductor impressions and the pallial line, some smaller muscle impressions are apparent. Such are those of the muscles which draw back the foot, or the anterior and posterior retractor muscles. These are small impressions, two in each valve, just above the big adductor impressions and in this mussel (*Lampsilis ligamentina*) confluent with the latter. The impression of the protractor, or the muscle which aids in protruding the foot, is usually quite distinct and just beneath the anterior adductor impression. Deep in the beak cavity and on the under surface of the cardinal teeth, or the bridge between cardinal and lateral teeth, are small pits which are the points of attachment of numerous small muscles that serve to elevate the foot. These last are the dorsal muscle scars referred to in systematic descriptions. (See Pl. XXI, fig. 1.)

DIVERSITY IN FORM.

Many modifications of the above description would have to be made for other species of mussels. The shell may be pear-shaped as in the niggerhead (*Quadrula ebenus*), or nearly circular as in *Quadrula circulus;* it may be very much inflated as in *Lampsilis capax* or in *L. ventricosa* (the pocketbook), or exceedingly compressed as in *Symphynota compressa*. In some the shell is not only greatly flattened from side to side but also extends upward in wings before and behind the beaks. Such species are given locally such descriptive names as pancakes, hatchet-backs (*Lampsilis alata*), or heel-splitters (*Symphynota complanata*). Some shells are proportionately very heavy, while others, included mostly in the genus Anodonta, the paper-shells or floaters, are so thin as to be useless for any present economic purpose. The Anodontas, adapted to live in lakes or close alongshore in streams, are further characterized by the entire absence of teeth.

Variations in thickness or in uniformity of thickness are important from the standpoint of the button makers, and so also are variations in the surface sculpture. Some forms are covered with protuberances or knobs in regular or irregular pattern, thus acquiring such common names as warty-backs or pimple-backs; while others have strong ridges running obliquely across the shell, as the three-ridge, *Quadrula undulata*, the blue-point, *Q. plicata*, and the washboard, *Quadrula heros*. One species, *Unio spinosus*, of Alabama, bears long sharp spines on the shell. Diversity of interior color has previously been alluded to. No satisfactory explanation of the colors of nacre has yet been offered. Certain species are almost always white-nacred, as the pimple-back, maple-leaf, and niggerhead. Others are white or pink, examples of the two colors living side by side. Some species have usually a deep purple or salmon nacre; but white-nacred shells of the same species may predominate in particular streams.

Variations in external color are conspicuous in any collection of shells even from the same mussel bed. Along with shells of uniform color, light or dark, we find shells of glossy surface and brilliantly rayed; the rays may be continuous or variously interrupted, sometimes composed of small zigzag markings forming striking and fantastic patterns. In short, the differences in form and color of shell are unlimited and could not be described, even within the limits of a systematic monograph.

THE SOFT BODY.

For observation of the body the mussel may be carefully opened by severing the adductor muscles close to one valve, preferably the left, and gently freeing the soft mantle from the shell as the knife blade is passed from one end of the shell to the other. Removing or bending back the upper (left) valve, the body of the mussel is seen to be almost completely enveloped in a thin mantle corresponding to the interior of the shell in form and size (Pl. XXI, fig. 1).

FORM AND FUNCTIONS OF THE MANTLE.

The mantle is composed of right and left sheets entirely free from each other except along the back where the two sheets are continuous not only with each other but with the body as well. The mantle is, in fact, a double fold from the back of the mussel draped over the body and lining the shell. A thin wing or dorsal extension of the mantle covers entirely the surfaces of the cardinal and lateral teeth and underlies the ligament.

The mantle is not of uniform character throughout but shows a broad border thicker than the central portion and somewhat muscular. This border along its inner line is attached to the shell through many fine muscle fibers, the attachment of which forms the pallial line on the shell. The border is muscular and, therefore, contractile; the lower or right mantle, which has not been separated from the shell, will have its edge contracted away somewhat from the margin of the valve; generally there is apparent a thin film of horny material which connects the edge of the mantle with the extreme edge of the shell. It is not infrequently the case that in separating the surface of the mantle from the shell a delicate transparent membrane is distinguishable, some parts of which adhere to the mantle and some parts to the shell. Unless, therefore, a rupture has occurred, the mantle normally is actually continuous at the margin with the outer surface of the shell, and probably organically but delicately connected to the inner surface of the shell over its entire surface.

The relations of the mantle as observed will have greater significance from a statement of its functions. Besides supplementing the gills in respiration and serving along its border as a sensory organ, a chief function of the mantle is the formation of shell. The extreme edge of the mantle secretes the horny covering of the shell, as also the ligaments and lunule, while the remaining mantle surface secretes the calcareous shell. For our purpose, accordingly, the mantle is a most significant organ. Diseases or other influences affecting the mantle frequently show effects in the shape, color, or quality of the shell, and it is in the mantle, probably, that all free pearls are produced. The mantle is not, however, the only portion of the mussel capable of forming shell. The two adductor muscles pass entirely through the mantle, having direct attachment to the shell. While the shell becomes thicker in other parts by the superposition of layer after layer of calcareous material from the surface of the mantle, the thickening of the shell against the muscles is in some measure, apparently, a function of the muscles themselves. It is not surprising, therefore, that these muscles also give rise to a large number of pearl formations, baroques, and slugs, but not, ordinarily, good pearls. No other parts commonly give origin to pearls, although it is reported that pearls have been found within the body. Baroque pearls and slugs are frequently found in the tissue just beneath the hinge line, but this is actually a part of the mantle.

The shell substance formed by the muscles is called hypostracum, and is largely horny in nature. Since each muscle occupies a nearly constant relative position regardless of the size to which the mussel attains, it is evident that in any adult individual the muscle traveled in the course of life history from the back to its latest position; the hypostracum, therefore, does not occupy a single spot but is a tapering vein passing through the nacre from the beak to the position of the muscle at any given time. Similarly the hypostracum of the pallial line is the margin of a thin stratum of like substance which extends from the beak or beginning of the shell and divides the nacre into two portions (p. 130).

The mantle has other functions of great importance. When the muscles are relaxed and the shell is gaping, the opening between the valves of the shell is largely closed by the apposed margins of the mantle. Nothing can enter between the valves of the shell without affecting the highly sensitive border of the mantle and thus giving warning to the animal, which may then contract its muscles and close the shell instantly. The nerves of the margin of the mantle are not only sensitive to tactile stimuli, but apparently are also connected with organs of something like visual function, so that the animal may close or open its shell under the influence of shadows or bright light.

It is the margins of the mantle that surround and form the two siphonal openings at the hinder end of the shell, through one of which water and food pass into the shell, while through the other water passes out, conveying the waste products. The lower of these two openings particularly is protected by projections of the mantle, in the form of papillæ or fimbriæ, which, being very sensitive, give warning of any objectionable character or content of the water.

OTHER CONSPICUOUS ORGANS.

Without disturbing the upper mantle two internal organs are distinctly evident. The heart is recognized by its throbbing action. It lies at the back just below the lateral teeth of the hinge and in front of the posterior adductor muscle. The rate of beating varies in different species and under different conditions but is generally under 20 pulsations per minute. The heart will continue to beat a long time after the shell has been opened. Near the anterior adductor is a greenish mass of tissue, the so-called liver or digestive gland, surrounding the white stomach. Through the transparent tissue, covering the chamber inclosing the heart, another portion of the alimentary tube is generally distinguishable. This is the rectum or hinder portion of the intestine which passes directly through the heart to discharge just above the posterior adductor muscle. The brownish tissue beneath the heart represents the organ of Bojanus, as it is called, with functions corresponding to a kidney.

To distinguish other organs the mantle must be folded back. The muscular mass of plowshare form and brownish white in color, constituting the anteroventral border of the body, is the foot. Several curtainlike flaps are conspicuous. Toward the forward end are two large earlike flaps, the labial palpi or lipfolds. They are easily torn in folding the mantle back, but if in good condition, it may seen that each of these palps is continuous, around the front end of the body, with the palp of the opposite side. Immediately in front of the body they are very narrow and lie one above and the other just below an exceedingly small opening, the mouth, which can be seen only by very careful examination.

The other two folds are much larger and rounded below. These are the gills, which extend from the anterior third of the body to the extreme posterior end. The inner is slightly the larger. The outer gill is connected above and on the outside to the mantle. Folding this one back, it is seen that it is attached also to the inner gill above. The inner gill on the inner side is attached to the body and, behind the body, to the inner gill of the opposite side. In many species the inner gill is partially free from the body. These gills, though thin, are really basketlike structures, containing chambers within, as will be described below.

INTERNAL STRUCTURE.

It is not the province of this paper to enter minutely into the internal anatomy. But the following epitomized statement of the structure of the animal is given to serve as a key to the understanding of the functions of the organism as a whole.

The digestive system comprises the mouth, with a short tube or gullet, leading from the mouth to the stomach; the dark brown digestive gland, or so-called liver, which surrounds the stomach; and the intestine, which is a long tube that leads downward from the stomach and coils upon itself behind the foot in a complex way, before bending upward to approach the back and extend posteriorly straight through the heart as the rectum, which opens just above the posterior adductor muscle. A long, slender flexible gelatinous rod, the crystalline style, is frequently found in the intestine; it serves a function in separating food from foreign particles and comprises a store of enzymes or ferments for use in the processes of digestion (Nelson, 1918).

The excretory system comprises a functional kidney with a bladder which discharges into the cavity surrounding the heart.

The circulatory system includes, as in higher animals, heart, blood, arteries, and veins. The blood of a mussel is colorless but maintains a regular circulation from the heart through certain arteries to many smaller vessels ramifying all through the body, returning by a main vein to the kidneys, thence to the gills and back through other veins to the heart to begin its course anew. The blood, however, which passes from the arteries to the mantle, returns, not through the kidneys or the gills, but directly to the heart.

The mantle and the gills constitute the chief respiratory organs, where the blood is aerated. The significance of the mode of circulation is evident. The venous blood returning from the body laden with waste products passes first to the kidney, thence to the gills to be cleared of impurities and freshened with oxygen, after which it returns to the heart in purified condition. The blood returning from the mantle requires no further purification or oxygenation before entering the heart.

Without a distinct brain, the body of the mussel is coordinated through a nervous system, consisting of three pairs of nerve centers, which are connected together by nerve cords. Two of these centers or ganglia lie one on each side of the gullet near the mouth, a second pair is in the foot, while the third lies just beneath the posterior adductor muscle. From these ganglia fine nerves are sent off to supply the various tissues and organs.

Though eyes and ears are not present, sensory organs are not entirely wanting. A small organ near the ganglia beneath the posterior adductor is supposed to serve to test the purity of the water. Another, the otocyst, is sometimes found near the ganglia in the foot and possibly serves as a balancing organ, by means of which the mussel may feel whether it is in horizontal or vertical position. Sensory cells are found along the border of the mantle, especially near the posterior openings for the passage of water. (See p. 87.)

The organs of reproduction comprise a large part of the body mass above the foot. The ova or semen are discharged through small openings on each side of the body into the chamber above the gills. In the case of the male the sperms are thence passed out with the respiratory (exhalent) current and set free in the water. They may be drawn into the female with the water of the inhalent current, to fertilize the ova perhaps as they are passed down from the suprabranchial chamber into the tubes in the gills where incubation takes place. In some species the reproductive tissue is brightly colored—orange, pink, or red.

STRUCTURE AND FUNCTIONS OF THE GILLS.

The gills, as the name would suggest, are primarily breathing organs. Nevertheless, they have an equal if not a greater function in food gathering, and, furthermore, in fresh-water mussels and in some other lamellibranchs, the gills have acquired a third office which is of coordinate importance with the other two. We have seen that the incubation of the egg takes place in the water tubes of the gills, a part or all of which may be filled with embryo mussels. The respiratory function of the gills of the female mussel must be greatly reduced during the period of incubation, and this condition is made possible by the fact that the mantle of the mussel plays an equal rôle with the gills in respiration. In becoming adapted to this function of protection and perhaps nourishment of the eggs and young, the gills of the female have undergone varied modifications in different species. In consequence, when gravid females can be examined, the gills of different mussels are often found to be more strikingly distinct than is the external form or any other obvious character. This is especially true when microscopic study of the structure of the gills can be made.

Whether or not, therefore, these differences are a true guide to relationships, the gills become one of the most convenient organs for distinguishing genera or species and serve as the most important basis of modern classification.

Some knowledge of the anatomy of the gills is necessary for proper comprehension of the life process of mussels in breathing, feeding, and reproduction.

The gills consist, as we have seen, of two platelike bodies on each side between the visceral mass and the mantle. We have thus a right and a left inner gill and a right and a left outer gill. Seen from the surface, each gill presents a delicate double striation, being marked by faint lines running parallel with the long axis and by more pronounced lines running at right angles to the long axis of the organ. Moreover, each gill is double, being formed of two similar plates, the inner and outer lamellæ united with one another below as well as before and behind but free at the top or dorsally. The gill has thus the form of a long and extremely narrow bag open above. Its cavity is subdivided by vertical bars of tissue, the interlamellar junctions, which extend between the two lamellæ and divide the intervening space into distinct compartments or water tubes, closed below but freely open along the dorsal edge of the gill. The vertical striation of the gill is due to the fact that each lamella is made up of a number of close-set gill filaments; the longitudinal striation, to the circumstance that these filaments are connected by horizontal bars, the interfilamentar junctions. At the thin free, or ventral, edge of the gill the filaments of the two lamellæ are continuous with one another, so that each gill has actually a single set of V-shaped filaments, the outer limbs of which go to form the outer lamella, their inner limbs the inner lamella. Between the filaments, and bounded above and below by the interfilamentar junctions, are minute apertures or ostia, which lead from the mantle cavity through a more or less irregular series of cavities into the interior of the water tubes. (After Parker and Haswell.)

The gills, then, which appear as thin plates, are really comparable to long baskets greatly flattened from side to side, the interior of the basket being subdivided into a series of deep tubes, all in one row. The surface of the basket, which is perforated by many pores visible only with a microscope, is covered with very minute paddles like fine flat hairs. The concerted action of these little paddles, called cilia, keeps driving the water from without the gill through the minute pores into the water tubes. Through these tubes the water passes upward into a chamber above the water tubes, called the suprabranchial chamber, and thence backward and finally out of the shell.

Since the cilia are habitually driving the water through the surface of the gills into the water tubes, it follows that there must be a regular stream of water entering the mantle chamber from without through the open valves, as well as an outgoing stream passing out from the chamber above the gills. These two streams are known as the inhalent current and the exhalent current, respectively. If a mussel is observed in undisturbed condition on the bottom of an aquarium (Pl. V, figs. 1 and 2), the two openings between the edges of the mantle are readily seen and the currents may easily be observed by introducing with a pipette into the water near each opening a little colored water. The coloring matter placed near the lower inhalent current is drawn into the shell, but that placed near the upper opening is driven forcibly away. The two pronounced currents, or rather two aspects of the same current, are, it may be repeated, formed entirely by the minute paddles surrounding the innumerable pores of the gill surfaces.

The gills themselves are living strainers in the course of this current, and as the water passes through them the material which serves as food is filtered out to be passed on to the mouth; at the same time, the blood in the minute vessels and spaces within the gill filaments and partitions is being purified and recharged with oxygen. The matter strained from the water becomes clotted with mucus and is driven along by the cilia over the surface of the gills to the labial palpi, where it is taken up and if suitable for food is passed on to the mouth, for the surfaces of the palpi as well as of the gills are covered by cilia or minute paddles, the combined action of which forms a wonderful mechanism for conveying the food from any point of the gill surface into the funnel-shaped mouth. The detailed working of this mechanism and the places and means of "switching off" undesirable matter form too complex a subject to be treated in this paper. (See Allen, 1914, and Kellogg, 1915.)

The course of the water is better understood after observing the mode of attachment of the gills. The outer lamella of the outer gill is attached to the mantle throughout its entire length, while its inner lamella and the outer lamella of the inner gill are attached together to the body. There is thus above each gill a small suprabranchial chamber just above the water tubes. Behind the body or visceral mass, however, the inner lamella of the right and left inner gills are attached together, and there is, therefore, a single large chamber above the four gills—the cloaca or exhalent chamber. The water, after passing through the pores of the gill surface, makes its course up the water tubes and backward by the suprabranchial chamber into the cloaca, to be passed thence out of the shell.[a]

It will be understood that the eggs and young borne in the water tubes of the gills, which become marsupial pockets, are most favorably located for respiration, being situated, as it were, in the respiratory current of the mother. There is, among the various species of the Unionidæ, great variation in the extent to which the gills are employed as marsupia (p. 139). In certain species the water tubes of all four gills are filled with eggs, in others only those of the outer gills receive the eggs, while in still others a portion of each outer gill is set apart as a marsupium. This may be the posterior half, the posterior third, or a few water tubes in the middle.

It is largely because of the great significance of the gills with their remarkably diverse functions of food collection, respiration, and gestation that the modifications both in the external form and in the histologic structure of the gills are important and serve so well as a basis of classification. Generally speaking, species in which all four gills serve as marsupia are considered lower or more primitive forms. Those in which the marsupia are most highly specialized are regarded as most highly developed.

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[a] The effect of the gills in filtering the water is made clear when one fills two jars with turbid river water after placing in each sufficient sand for a mussel to become embedded. If one or two mussels are placed in one of these jars, the water will become clear in a comparatively short time.

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PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF SALMONOID FISHES AND THEIR SIGNIFICANCE IN FISH-CULTURAL PRACTICES

By William Converse Kendall

From BULLETIN OF THE BUREAU OF FISHERIES, Volume XXXVII, 1919–20

Document No. 901 *Issued March 28, 1921*

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CONTENTS.

❧

Page.
Introduction........ 185
Abdominal viscera........ 185
  Alimentary tract........ 187
  Liver........ 187
  Kidneys........ 187
  Pancreas........ 187
  Spleen........ 187
  Air bladder........ 187
  Gonads........ 187
The peritoneum and supporting membranes of the viscera........ 187
  Histological structure and embryonic development........ 187
  The dorsal mesentery of Salmonidæ........ 188
  The ventral mesentery........ 188
Structure and development of genital organs of fishes in general........ 188
Observations upon ovaries and ovarian membranes of Salmonidæ........ 191
Oviducts of Salmonidæ........ 194
Peritoneal membranes, ovaries, and oviducts of Coregonidæ........ 197
Ovaries, ovarian membranes, and oviducts of smelts........ 197
Summary........ 200
Relationship of salmonoid fishes, ganoids, and elasmobranchs as indicated by the oviducts........ 200
Relation of the anatomical facts to fish-cultural practices........ 203
List of works consulted........ 206

PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF SALMONOID FISHES AND THEIR SIGNIFICANCE IN FISH-CULTURAL PRACTICES.

⁂

By WILLIAM CONVERSE KENDALL,
Scientific Assistant, U. S. Bureau of Fisheries.

⁂

INTRODUCTION.

The observations embodied in the present discussion were begun several years ago and have been carried on intermittently to the present time. The study has been attended by various difficulties. It has been almost impossible to obtain perfectly preserved specimens in which the internal organs had not been more or less deranged or mutilated. The membranes in question, being very delicate, are easily torn or broken in handling prior to or during dissection and are liable to disintegrate unless well preserved. These facts and others, together with erroneous ideas derived from published references to these structures, have occasioned many uncertainties which have taken a long time to clear up. Since the ovaries undergo many changes of both external and internal appearance, as well as of position, at no time in their growth or development can they be said to be exactly the same as at any other time. After the ova are shed, in those species which normally survive the spawning period, the ovaries undergo many retrogressive changes. Furthermore, the conditions are not always uniform in the same species. Somewhat different conclusions might be reached from observations upon examples representing one or two periods of development only than from a more complete series. Therefore it has required many individuals to permit of an exact determination of conditions. In fact it was only after careful dissection of more than a hundred American smelts that one which seemed to conform to the conditions in the European smelt, as described by Huxley (1883), was found. Probably the failure of the anatomists, to whom reference is made in this paper, to recognize the conditions which are herein described, is attributable to some such facts as the foregoing.

As this paper is primarily intended for fish-culturists and those unfamiliar with anatomy, definitions of the principal abdominal structures precede the discussion. Although desirable, it has been impossible to entirely eliminate scientific phraseology.

At the end of this paper is given an alphabetical list of the authors and works consulted. In the text of this discussion these works are referred to by author and date of publication.

ABDOMINAL VISCERA.

The abdominal viscera comprise the greater portion of the alimentary tract, secretory, excretory, and reproductive organs, together with certain nervous and vascular connections. The present discussion is principally concerned with the supporting and

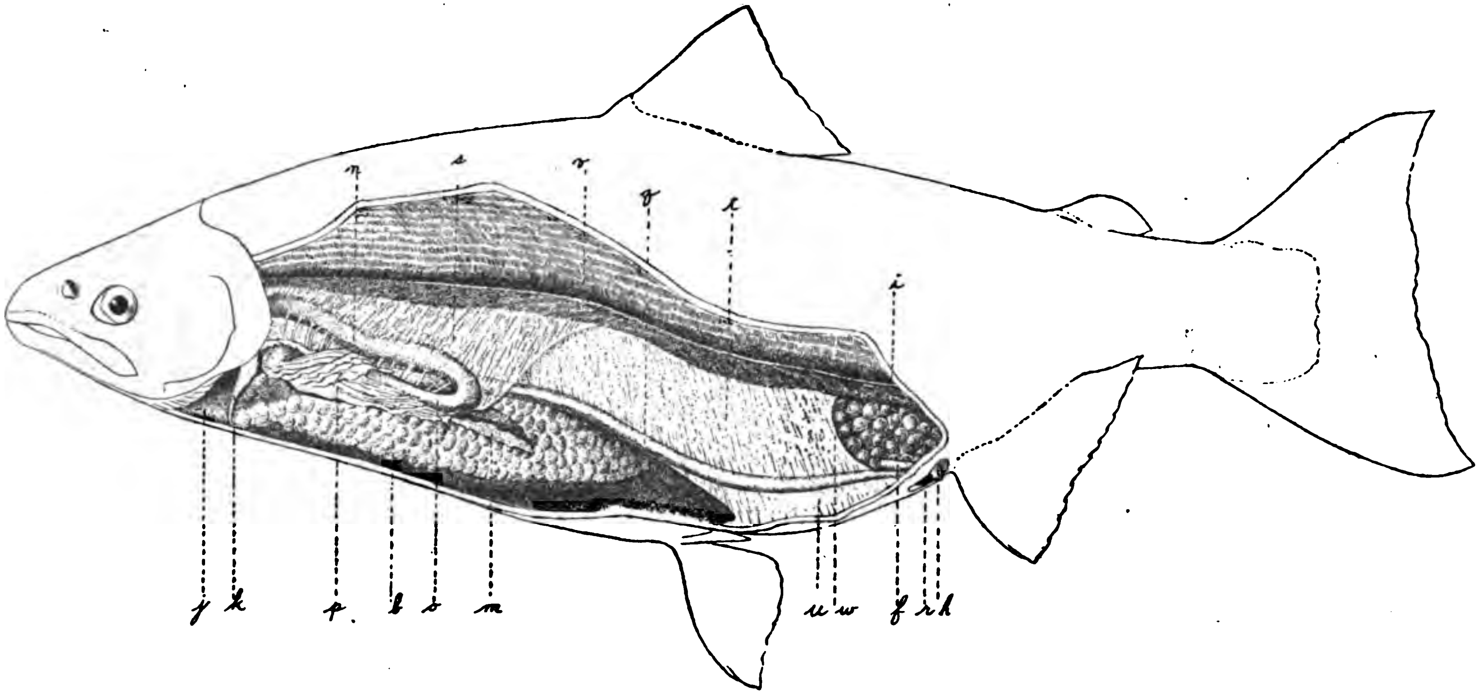

FIG. 1.—Drawing made by Mrs. Effie B. Decker, from a specimen of *Oncorhynchus nerka*, 24¾ inches long, collected by Ernest P. Walker, salmon inspector, Wrangel, Alaska, at the mouth of a small stream tributary to Stikine River, some ten miles from mouth of river, August 12, 1917; about one-third natural size; *b*, left or inner side of right ovary; *f*, left side of oviducal channel, anteriorly severed; *h*, genital papilla and pore; *i*, free eggs in oviducal channel; *j*, heart; *k*, anterior septum or diaphragm, separating the abdominal cavity from the anterior body cavity; *m*, spleen, the left ovary rests in the upper groove; *n*, cardiac end of the stomach; *o*, pyloric arm of stomach extending forward to the junction with the pyloric end of the intestine; *p*, pyloric cæca or appendage with attached adipose tissue arising from the pyloric ends of stomach and intestines and lying upon the pyloric arm of the stomach and resting against the ovaries; *q*, intestine; *r*, anus; *s*, gastric mesentery; *t*, intestinal dorsal mesentery; *u*, ventral mesentery; *v*, left longitudinal side of air bladder; *w*, posterior termination of the dorsal mesentery.

investing membranes (peritoneal membranes) associated with the digestive and reproductive systems.

ALIMENTARY TRACT.—In the Salmonidæ the alimentary tract forms a loop within the anterior half of the abdominal cavity or cœlome, so that three portions are recognized: The stomach (fig. 1 *n*), a thick-walled arm extending backward to the point where it makes a sharp bend and as the pyloric arm (fig. 1 *o*), more or less covered by the mass of pyloric appendages or cæca (fig. 1 *p*), extending forward to the posterior surface of the liver, where another sharp bend occurs and from which the intestine (fig. 1 *q*) extends back to the vent.

LIVER.—The liver (fig. 2 *l*) is relatively massive and fills nearly the whole anterior end of the abdominal cavity, on each side more or less overlying the other anterior viscera.

KIDNEYS.—The kidneys lie immediately below and in contact with the dorsal surface and extend from the anterior septum or diaphragm (fig. 1 *k*) to the region of the vent.

PANCREAS.—The pancreas is an elongated lobulated digestive gland, more or less embedded in fat, lying on the upper surface of the stomach and often more or less upon the upper surface of the intestine posteriorly to the stomach.

SPLEEN.—The spleen (fig. 1 *m*) is a dark-colored lymphoid or fluid gland of variable size, irregularly a three-surfaced pyramid, situated close behind the posterior curve of the stomach.

AIR BLADDER.—Immediately below the kidney mass, in contact and approximately coextensive with it, is the air bladder.

GONADS.—The reproductive glands of the Salmonidæ are paired, more or less symmetrical organs, one on each side of the abdominal cavity.

THE PERITONEUM AND SUPPORTING MEMBRANES OF THE VISCERA.

The peritoneum is a serous membrane lining the adbominal cavity and sending out various folds which support and more or less attach to each other the visceral organs. Anteriorly, in conjunction with other tissues, it forms a partition analogous to the diaphragm of higher vertebrates, separating the adbominal cavity from that part of the cœlome containing the heart, gill, esophagus, etc. (fig. 1 *k*). A fold extending to the digestive organs, infolding and forming suspensory membranes, or filamentous and ligamentous attachments, is called the mesentery (fig. 1 *s* and *t*).

HISTOLOGICAL STRUCTURE AND EMBRYONIC DEVELOPMENT.—According to Bridge (1904), the peritoneum histologically consists of a stratum of connective tissue, supporting on its free surface an epithelial stratum (cœlomic epithelium). Primarily, the investing peritoneum is continued both dorsally and ventrally into bilaminar suspensory folds, the dorsal and ventral mesenteries, which extend to the mid-dorsal or mid-ventral line of the abdominal cavity. The two layers then separate and become continuous with the parietal layer of peritoneum lining the whole of the inner surface of the body wall. Embryologically, the two mesenteries owe their formation to the fusion above and below of the mesenteron of the contiguous walls of two laterally and primarily distinct cœlomic cavities. The dorsal mesentery in the adult is occasionally complete, as in the myxinoid Cylostomata and in a few teleosts, but much more frequently is reduced by absorption to anterior and posterior rudiments, or to a series of isolated bands, or even, as in the lamprey (Petromyzon), to a few filaments accompanying the intestinal blood vessels.

THE DORSAL MESENTERY OF SALMONIDÆ.—In adult Salmonidæ the supporting membrane of the alimentary tract diverges from near the longitudinal median line of the peritoneal covering of the air bladder and is attached to the upper surface of the canal as follows: From the diaphragm (fig 1 *k*) and along the mesial line of the air bladder (fig. 1 *v*), a fold (fig. 1 *s*) is sent out to the upper surface of the stomach on which it ends near the posterior bend or sometimes extends to the spleen (fig. 1 *m*). The pyloric arm has no supporting membrane, but is connected to the cardiac arm of the stomach by filamentous bands, though sometimes anteriorly there may be a trace of membrane. Again, beginning near the diaphragm is another fold (fig. 1 *t*), which, attached to the backward prolongation of the intestine, extends nearly to the vent in the female and quite to the vent in the male.

THE VENTRAL MESENTERY.—Concerning fishes in general, Bridge writes that the ventral mesentery is rarely present and, if present, is never complete. In Lepidosteus a ventral mesentery is said to be present in connection with that part of the intestine which contains the spiral valve. In Protopterus, and also in Neoceratodus, there is a well-developed ventral mesentery in relation with the greater part of the length of the intestine, although in the former Dipnoid its continuity is interrupted by one or two vacuities, and in the latter the mesentery is incomplete posteriorly. A ventral mesentery is also present in the intestinal region of some of the Murænidæ among teleosts, but no mention is made of it in Salmonidæ.

I have examined four species of Oncorhyncus (*O. kisutch*, *O. gorbuscha*, *O. tschawytscha*, and *O. nerka*); several species of Salmo (*S. salar*, *S. sebago*, *S. trutta*, *S. gairdnerii*, and *S. shasta*); and several Salvelinus (*S. stagnalis*, *S. aureolus*, *S. oquassa*, *S. marstoni*, *S. malma*, *S. kundsha*, and *S. fontinalis*), all of which possess a certain extent of ventral mesentery (fig, 1 *u*). Its anterior ventral insertion is a little behind the base of the ventral fins, and the corresponding intestinal insertion somewhat in advance of the ventral insertion, thus presenting a vertical concave edge toward the front. This mesentery in its ventral and intestinal attachments extends to the posterior end of the abdominal cavity. According to Felix (1906) the embryo salmon has a complete ventral mesentery.

By these vertical dorsal and ventral mesenteries and the intestine to which both are attached, about one-third of the abdominal cavity is posteriorly divided into two lateral longitudinal chambers, with a posterior communicating aperture of varying length, but always short, in the dorsal mesentery above the intestine of the female.

STRUCTURE AND DEVELOPMENT OF GENITAL ORGANS OF FISHES IN GENERAL.

The suspensory portion of the ovarian membrane is known as the mesovarium, or mesoarium, and that of the spermary as the mesorchium. Morphologists state that the gonads of the majority of teleosts are completely enveloped by the peritoneal membrane and that the ova and sperm of oviparous forms are conveyed to the exterior of the body cavity by closed canals or tubes composed of the same enveloping membrane extending from the gonad to the genital pore (fig. 2 *h*). The previous state of knowledge regarding especially the ovarian membranes of Salmonidæ is well indicated by the following review of the opinions or statements of principal writers.

One authority (Wiedersheim, Parker, 1897) states that the male and female gonads of teleosts, closely correspond with one another as regards position and the arrangement of their ducts. Dorsal and ventral folds of the peritoneum are developed in connection with the elongated ovary, and these in most cases meet along its outer side, so as to inclose a portion of the cœlome, and thus convert the ovary into a hollow sac, blind anteriorly, on the inner folded walls of which the ova arise; this sac is continued backward to form the oviduct, which is generally short and fuses with its fellow to form a tube or "ovipositor"; or the ducts may communicate with the urogenital sinus.

The same authority describes the development of the ovary as originating in at first undifferentiated cells of cœlomic or peritoneal epithelium on the dorsal side of the body cavity at either side of the mesentery in which the adjacent mesoblastic stroma penetrates. Into the stroma of an ovary thus formed, the cells of germinal epithelium grow in the form of clustered masses; some of which cells increase in size more than others, giving rise to ova, while the smaller cells form investment of follicle around each and serve as nutritive material.

From the foregoing it is understood that the ovaries of most teleosts are derived from folds of the peritoneum, usually one on each side of the body cavity, and, as a rule, are closed sacs consisting of an outer enveloping membrane and inner laminæ of ovigerous stroma. Each egg is inclosed in a follicle from which, as it ripens, it breaks out into the inner or central cavity of the ovary and makes its exit from the fish by the way of a tube, or oviduct, of the same membrane and the genital pore.

Some exceptions to this arrangement have been noted. Something over 90 years ago, Rathke (1824) described the ovarian membranes of certain salmonoid fishes, and nearly 60 years later Huxley (1883) reviewed Rathke's work, from which he quotes as follows:

> In certain fishes the oviducts have entirely disappeared; this is the case in the eel, the sturgeon, *Cobitis tænia*, and in the lamprey. In others, however, such as the higher kinds of salmonoids, there extends back behind each ovary a narrow band which may be regarded as the remains of an oviduct. In all these fishes, therefore, the central abdominal cavity must take the place of an oviduct, as it receives the eggs when they are detached, and allows them to make their exit by a single opening at its posterior extremity.

Still quoting from Rathke, Huxley continued to the effect that, while a proper oviduct is absent from the Salmonidæ, there is an analogue of that structure, consisting of a flat, narrow band, commonly arising at the upper and posterior end of a platelike ovary, gradually diminishing in width backward, and finally becoming lost toward the end of the abdominal cavity. It was stated that in the salmon proper it disappears upon the air bladder opposite the commencement of the last fifth of the abdominal cavity; in the fresh-water trout on the sides of the intestine not far from the anus; in the whitefishes (Coregoni) on the intestine close to its end.

In describing the ovary of the European smelt *Osmerus eperlanus*, which was at that time regarded as a member of the salmon family, Huxley stated that in all essentials of the structure of the ovigerous portion or body it agreed with that of the other Salmonidæ. It was said to have the form of a half-oval plate, with the curved edge ventral and the straight edge dorsal. To the latter a narrow mesovarial fold of the peritoneum was said to extend "from that part of the dorsal wall of the abdominal cavity which corresponds with the ventral surface of the air bladder" and the line of attachment to be parallel with that of the mesentery and a little distance from it. The ovary, described as a broad, thin plate, was stated to have its inner surface covered by the peritoneum, which is continued over the ventral edge, ending about a third or fourth of the height of the outer face by a well-defined margin and its outer face "to give rise to a great number of ovigerous lamellæ of broadly triangular form, which are disposed transversely to the length of the organ and perpendicularly to the body." Huxley went on to say that superficially the ovary appears to be laminated only above the reflected membrane, but that transverse section revealed that the ovigerous laminæ pass under the band to the ventral wall and that their outer edges are attached to the band.

In the Salmonidæ, then, according to both Rathke and Huxley, ovigerous laminæ without peritoneal covering occupy the outer surface of the pendent mesovarial fold, thus constituting the ovary, from which as they ripen and burst from their investing follicles, the ova fall into the abdominal cavity. As will be seen later, the foregoing observations pertain to only one stage, that of a collapsed and retracted ovary.

Prior to Huxley's description of the oviduct of the smelt, no salmonoid was supposed to have such a structure. In the smelt, according to Huxley, the mesovarial fold continues backward from the posterior end of the ovary to the oviducal apertures, while laterally it passes into the peritoneal lining of the lateral wall of the abdomen, ending in a free concave edge immediately behind and on the outer side of the posterior extremity of the ovary. It thus forms the ventral boundary of a passage which opens in front by a wide ostium into the abdominal cavity. As the posterior end of the right ovary lies very far behind that of the left ovary, it follows, Huxley says, that the right ostium is equally far behind the left. The mesentery, he continues, terminates by a free posteriorly concave edge just opposite the level of the posterior end of the right ovary; and, behind this free concave edge of the mesentery, the left and right passages unite in a short but wide common chamber which opens externally in the middle line behind the anus and in front of the urinary outlet.

It appears that it must be to this structure in the smelt that all subsequent writers refer when mentioning oviducts of Salmonidæ, many regarding the smelt as a member of this family.

This idea that the salmonoids have no oviducts and that the ova are deposited free in the abdominal cavity has been handed down to the present day in all literature pertaining to the subject. Owen (1866) said that the salmon is an example in which the ova are discharged by dehiscence into the abdominal cavity and escape by the peritoneal outlets, as in the eel and lamprey, and that the free surface of the stroma of the ova is exposed.

Gegenbaur (1878) said that in the Salmonidæ the eggs are passed into the abdominal cavity and are evacuated through the abdominal pore.

Günther (1880) wrote that in some families of fishes the ovaries are without closed covering and without oviduct, as in Salmonidæ, Galaxidæ, Notopteridæ, Murænidæ, and others. He stated that the surface of such an open ovary—as, for instance, that of the salmon— is transversely plaited, the ova being developed in capsules in the stroma of the laminæ; after rupture of the capsules, the mature ova drop into the abdominal cavity and are expelled by the porus genitalis.

Day (1887) makes practically the same statement, saying that the ovaries are symmetrical organs and destitute of a closed covering, while their internal surface is lined with stroma and transversely plaited. Here, he said, the development of the eggs takes place, each of which is invested by a fine membrane, by which they hang suspended to the ovary, the length of the pedicle decreasing as the egg augments in size. But as the ovaries are destitute of oviducts it necessarily occurs, he continues, that when the investing membrane bursts, the ovum falls into the abdominal cavity, from whence it is extruded through the abdominal pore.

Jordan and Gilbert (1882) and Jordan and Evermann (1896) make similar statements: "Ova falling into the cavity of the abdomen before exclusion."

In discussing the brown trout (*Salmo fario*) as an example of "subclass III Teleostomi" Parker and Haswell (1897) state that the ovaries extend the full length of the abdominal cavity and are covered with peritoneum on their inner or mesial faces only, and that, when ripe, the numerous ova are discharged from their outer faces into the abdominal cavity. They then go on to say that there are no oviducts, but that the anterior wall of the urogenital sinus is pierced by a pair of genital pores through which the ova make their way to the exterior.

A previously cited authority (Wiedersheim, Parker, 1897) wrote that the ovary of some teleosts is solid and that the ova are shed into the body cavity. The oviducts of the smelt (Osmerus) and capelin (Mallotus) were referred to as peritoneal funnels having open cœlomic apertures close to the ovaries, into which the ova pass. In the case of other Salmonidæ, the Muraenidæ, and Cobitis, it was stated that these peritoneal funnels are shorter and even absent, the ova then being shed into the urogenital sinus through paired or single genital pores.

After describing the genital structures of the Salmonidæ, Bridge (1904) states that in all instances the eggs are set free from the ovaries into the cœlome, whence they escape through the peritoneal funnels or genital pores. The foregoing statements reveal the influence of Rathke and Huxley upon all subsequent interpretations of the structures.

The only teleosts besides Salmonidæ mentioned by Rathke as possessing no oviducts were two species of loach (*Cobitis barbatula* and *C. tænia*) and the eel. Regarding these Huxley says that in *Cobitis barbatula* the single ovary has an oviduct of the same character as other Cyprinoid fishes, but that he had not examined *C. tænia*, about which, in other parts of his memoir, Rathke's statements were full and precise.

Inasmuch as one of the species of the loach was found to have an oviduct, it is quite possible that the other has also. If such is the case, according to Rathke, the only supposedly oviductless species, besides the Salmonidæ, left without such a duct is the eel. However, a few other fishes have since been stated to be oviductless.

The salmonoids, according to the authorities mentioned, appear to occupy almost a unique place among teleosts; but in the discussion which follows I hope to show that their position is not as anomalous as from the foregoing it would seem to be.

OBSERVATIONS UPON OVARIES AND OVARIAN MEMBRANES OF SALMONIDÆ.

The two ovaries in each of the salmonoids which I have examined are never exactly symmetrical in form or of the same length. They have a general primary shape which is maintained, but in their growth and enlargement such modifications of shape and position as occur are largely determined by contiguous internal organs and the abdominal walls. Each ovary is suspended by a membrane (fig. 2 *c*) originating in the dorsal

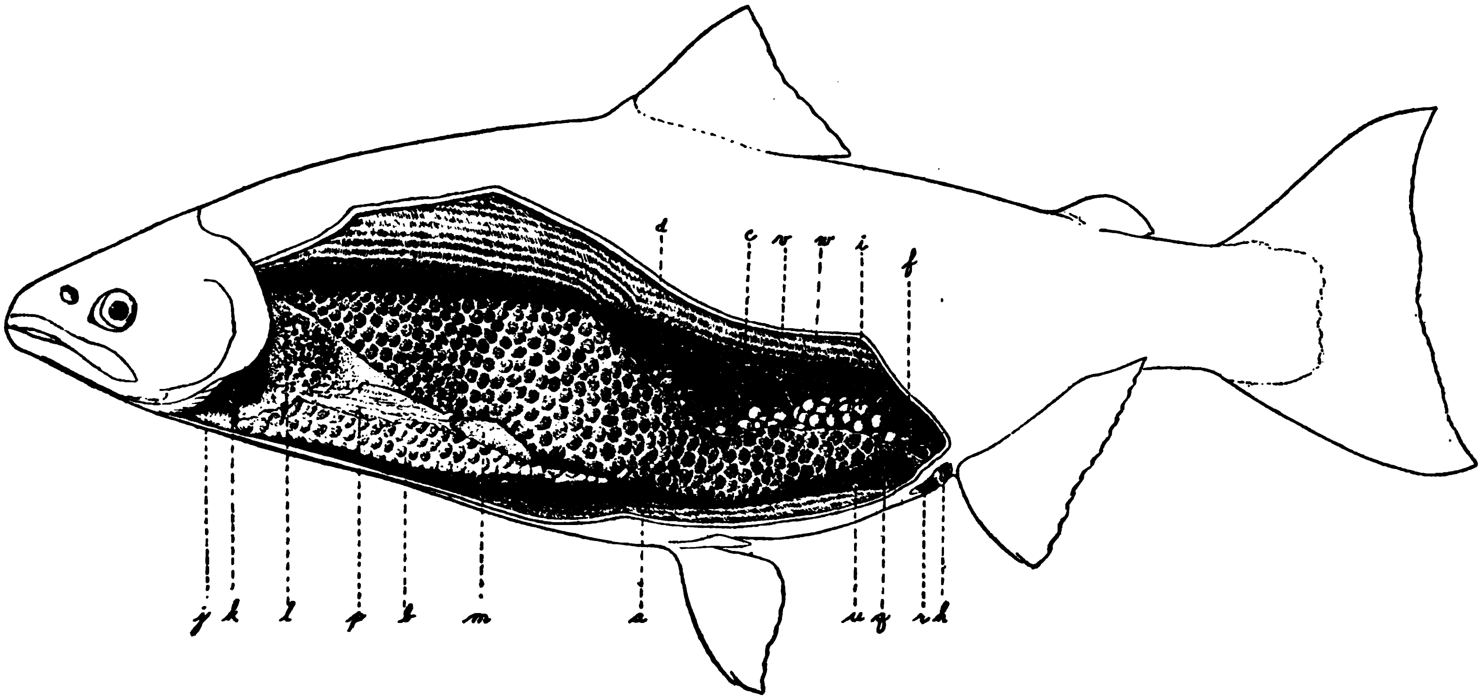

FIG. 2.—Drawing from the same specimen as shown in fig. 1. *a*, Left ovary and containing membrane (somewhat pulled down, revealing ova posteriorly); *b*, right ovary containing membrane showing below left ovary, fish somewhat oblique, opening toward observer; *c*, mesovarium, with air bladder showing through; *d*, outer edge of ovarian membrane; *f*, left side of oviducal channel; *h*, genital papilla and pore; *i*, free ova in oviducal channel; *j*, heart; *k*, diaphragm; *l*, liver; *m*, spleen; *p*, pyloric cæca; *q*, intestine; *r*, anus; *u*, ventral mesentery; *v*; posterior end of intestinal mesentery with confluent mesovarium; *w*, air bladder.

peritoneum at the side of the air bladder. This membrane covers the surface of the ovary which faces the longitudinal axis of the body cavity. From its posterior end a membranous band, which is a continuation of the mesovarium and ovarian covering extends toward the posterior end of the abdominal cavity. Up to this point the conditions are as stated by the anatomists previously cited.

An immature ovary shows that its membrane not only covers the mesial or inward surface as described, but envelops the entire organ. The edge of the membrane, which was stated to mark the termination of the covering at or near the lower margin of a platelike ovary, passes up over the outer surface and is in contact with the membrane of the inward surface. At this time the ovary has much the same general external appearance as that of the other isospondylous teleosts. At a later period, beginning at the posterior end of the ovary, the edge of the membrane of the outer surface to some extent parts from the membrane of the inward surface, leaving a narrow area of ova without attached membranous cover. The area thus uncovered gradually widens and extends forward as the ovary increases in size. Even at maturity the egg surface is to a certain extent infolded in membrane (fig, 2 *a*), due to the fact that the suspensory mesovarium does not hang vertically but, from its origin at the side of the air bladder slants inward toward the axis of the body cavity, and the egg surface is tipped over so that its

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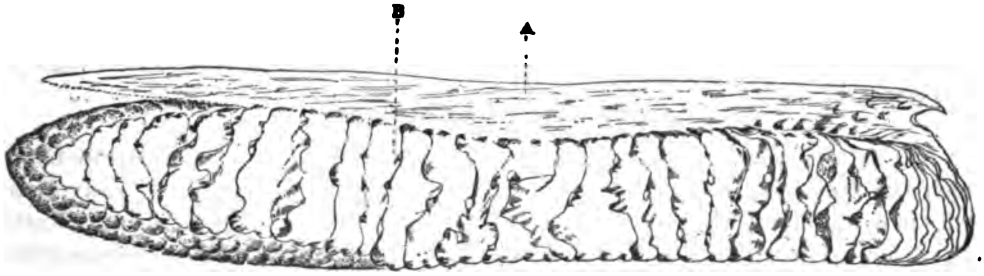

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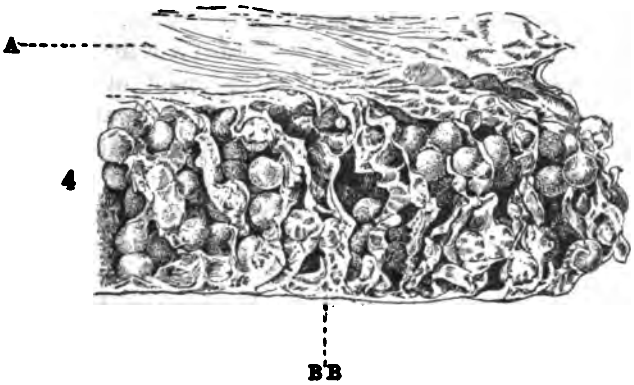

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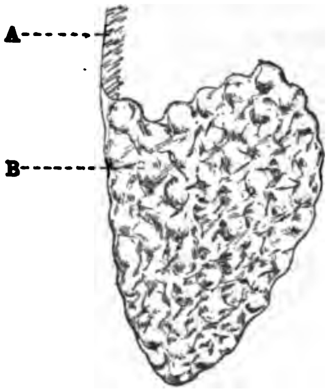

FIG. 3.—Upper view of left ovary, with most of ova removed, showing cross septa and membrane extending up over the forward end. *A*, mesovarium from which ovary is turned downward to show upper view.

FIG. 4.—Dorsal view of a section of same ovary as in fig. 3 from the region of *B*, *BB* representing the same cross septum as *B* in figs. 3 and 5. Some ova have been removed, others are shown still in the follicles. *A*, mesovarium.

FIG. 5.—Cross septum (*B*) in upright position. In natural position, mesovarium (*A*) would incline to right, and upper edge of septeum (*B*) to left. Impressions of ova shown in septum.

Figs. 3 to 5 drawn by Mrs. Effie B. Decker.

face is against the mesovarium. This position brings what has been termed the upper edge of the ovary downward, so that it is actually considerably lower than the supposed lower edge (fig. 2 *d*), so far as there is any edge. In other words, even the ovary is not platelike, but the supposed plate is folded in such a manner that it may be said in a general way to be boat-shaped with a decided list to starboard or port according to whether it is the left or right ovary. Posteriorly the exposed egg surface is usually proportionally wider and sometimes actually wider than at the anterior end. In fact, the anterior end is permanently covered to some extent by membrane, or to continue the boat simile, it is decked over forward (fig. 3). Furthermore, the ovigerous stroma, which has been stated to be arranged in vertical laminæ, transversally and somewhat diagonally connects the two sides, dividing it into transverse compartments (figs. 3 *B*, 4 *BB* and 5 *B*).

OVIDUCTS OF SALMONIDÆ.

As relates to the vestigial or rudimentary[1] oviduct in the form of a narrow band to which the previously quoted anatomists have referred, it is necessary to say that it varies in extent according to the species and does not terminate as described by Rathke, but, without close examination, in an immature, or spent, fish it might be so interpreted.

In a silver salmon (*O. kisutch*), which was unripe, but approaching breeding condition, the lesser backward extent of the ovary resulted in a relatively longer band than was evident in ripe fish, by which the general arrangement is more clearly defined. This band (fig. 6 *e*) arises from the posterior end of the ovary whence backward it is an extension of the ovarian covering and the mesovarium. The line of attachment of the mesovarium (fig. 6 *c*) to the air bladder extends obliquely inward and backward toward the median line of the air bladder until it attains a point near the termination of the mesentery at the anterior end of the communicating aperture above the intestine previously mentioned (fig. 6 *w*). Here the mesovarium, as such, apparently ends. Fusing with the mesentery at a corresponding point on the upper surface of the intestine, the mesovarian membrane joins the membrane of the opposite side, forming a single band, which is attached to and extends along the intestine backward. The outer edge of this band, at the posterior end of the ovary, in unripe or immature fish at least, appears to fold over onto the band forming a sort of hem to the edge (fig. 6 *f*), later becoming the outer edge of the trough, which is supported by the lateral walls of the narrow posterior portion of the abdominal cavity. This outer edge pursues a similar direction to the air-bladder attachment of the mesovarium to the point where the mesentery and mesovarium terminate, whence it takes a course parallel with the middle or line of attachment of the band to the intestine. Its outer edge remains free, and the fold, though becoming narrower, is continued to within a short distance from the genital pore, where it seems to vanish. The membranous band is deflected to either side and becomes attached to the lateral abdominal wall (fig. 6 *g*). Thus from each ovary a troughlike oviduct passage is formed as far as the termination of the mesentery of the intestine, the two passages then merging into one which, not far from the outlet, spreads out and joins the lateral wall on each side. This terminal structure would appear to be a reduced homologue of the so-called funnel described by Huxley in the case of the smelt.

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[1] Wiedersheim (Parker), 1897, p. 360, referring to these structures, says: "It is uncertain whether the latter is the primitive arrangement among teleosts, or whether the peritoneal funnels represent reduced oviducts."

As the ova approach maturity,[1] the left ovary is nearly or quite always the longer, and it extends, tapering, to the posterior end of the abdominal cavity (fig. 7 *a*). About at the point where the mesovarium as a suspensory membrane ends and forms the beginning of the trough mentioned (fig. 7 *w*), the posterior extension of the ovary has no membranous attachment to the trough, but has a free fold or flap of mesovarial or ovarian membrane along its upper inner side which narrows posteriorly to the end

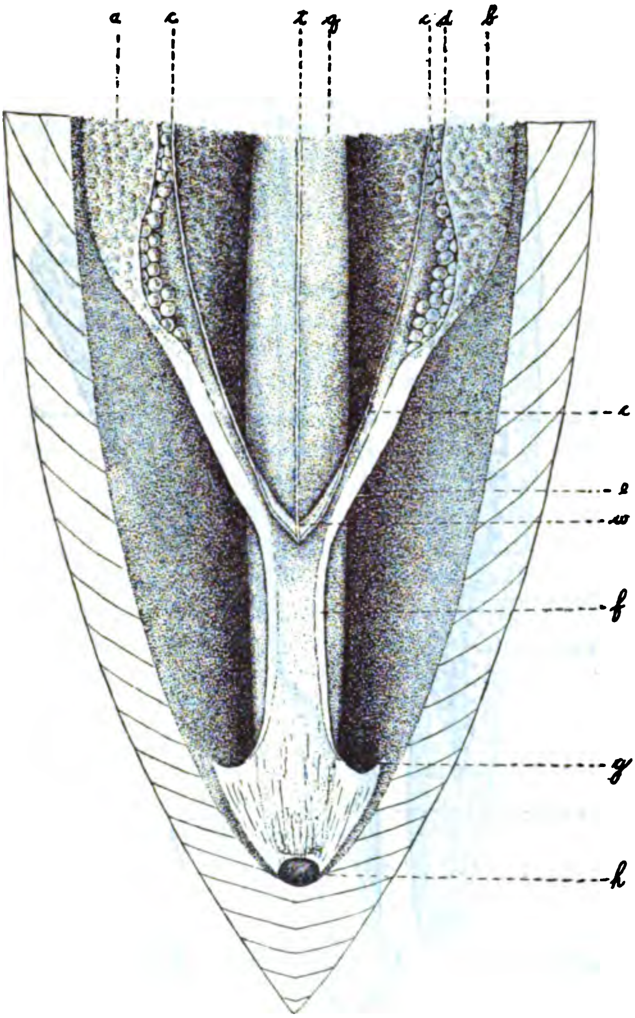

FIG. 6.—Drawing by Mrs. Effie B. Decker from a specimen of *Oncorhynchus kisutch*, 26 inches long, from Ankon Slough, Alaska, July 10, 1917, collected by Ernest P. Walker, salmon inspector. Dorsal view of the posterior end of the abdominal cavity, the abdominal wall somewhat spread out. In natural position this portion of the abdominal cavity is very narrow, and the walls closely approximate. The intestine is laterally flattened and compressed so that it does not show beyond the edges of the superimposed membrane, and the edges of the membrane are turned upward, forming a trough. *a*, Left ovary; *b*, right ovary; *c*, upper severed edge of mesovarium; *d*, outer edge of ovarian membranous covering; *e*, fold or free border of the posterior extension of ovarian membrane, which joins with the other on median line of intestine forming an oviducal channel or trough; *f*, oviducal channel, combination of *e* from both sides; *g*, lateral deflection and junction of oviducal membrane with abdominal wall; *h*, genital pore; *q*, intestine; *t*, severed dorsal intestinal mesentery; *w*, posterior end of severed mesentery.

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[1] As observed in one specimen each of Atlantic and humpback salmon.

of the ovary where it again completely infolds the organ (fig. 7 *c*). This flap and the inner side of the ovary probably lie in the trough on the top of the intestine, and the greatly narrowed or pointed end of the ovary rests on the bilateral expansion formed by the deflection of the edge of the trough to the abdominal wall (fig. 7 *g*).

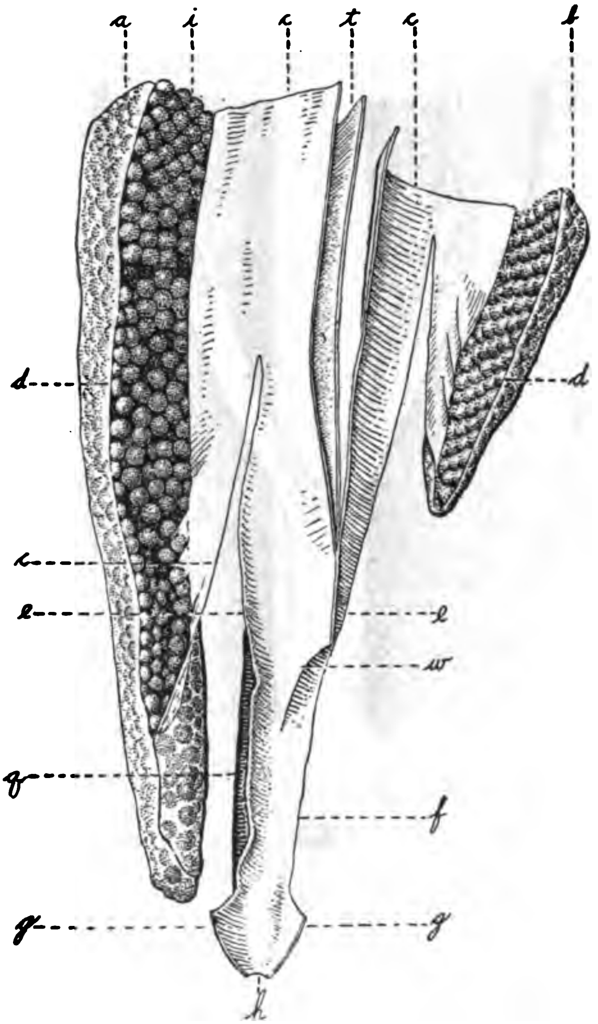

FIG. 7.—Drawing by F. E. Prior, from dissection of a specimen 23¼ inches long, from the Penobscot River, Me. Dorsal view of a spread-out section of posterior portion of abdominal viscera and membranes of nearly ripe Atlantic salmon (*Salmo salar*). *a*, Left ovary, *b*, right ovary, turned away from mesovarium showing eggs not covered by ovarian membrane; *c*, mesovaria laid back from normal position on surface of otherwise uncovered eggs; *d*, outer edge of ovarian membrane; *e*, fold or free borders of mesovaria which unite posteriorly to form the oviducal channel; *f*, oviducal channel continuation of *e*; *g*, posterior lateral expansion of oviducal channel, each side of which unites with peritoneum of the lateral walls of the abdominal cavity; *h*, genital pore; *i*, eggs not covered by ovarian membrane; *q*, intestine; *t*, dorsal intestinal mesentery; *w*, posterior end of intestinal mesentery with confluent mesovaria.

The right ovary (fig. 7 *b*), always somewhat shorter, seldom extends in this manner much behind the common opening above the intestine, and accordingly it may or may not have some extent of membranous flap as just described. The ova apparently run along the fold on the inner side of the ovary, and hence into and along the trough mentioned.

These backward extensions of the ovaries are formed by the maturing and enlarging ova filling the previously crowded interlamina spaces at the posterior end of the ovary (fig. 3), thus stretching it longitudinally.

PERITONEAL MEMBRANES, OVARIES, AND OVIDUCTS OF COREGONIDÆ.

A number of specimens of each of the genera Coregonus and Leucichthys were examined.

The arrangement of the visceral organs was similar to that of the Salmonidæ, but no ventral mesentery was observed. The ovaries and oviducts were much as in Salmonidæ.

OVARIES, OVARIAN MEMBRANES, AND OVIDUCTS OF SMELTS.

As has been seen, according to Huxley, the smelts were supposed to have free ovaries and oviducal funnels, while the salmonids were stated to have free ovaries and only narrow bands, or vestigial homologues of oviducts. My examination of many smelts reveals that, while Huxley was correct concerning the oviducal structures, his interpretation of the ovary was not in accord with all of the facts. He probably accurately described what he saw under certain limited conditions. I previously remarked that at no time in their development can the ovaries be said to be exactly the same as at any other time. This is particularly true as concerns the ovaries of the smelt (*Osmerus mordax*). If the ovary of a spent fish, or one from which the eggs have been removed or washed out, as Huxley stated of his example, is examined, the condition is likely to be as represented by Huxley. The ovary then is in a collapsed, flabby condition, or more or less shrunken state. When the ovaries are full-grown, just before spawning time, but before any ova have been discharged into the oviducts, they exhibit an entirely different appearance. As described of Salmonidæ, the air bladder is attached to each side of the dorsal portion of the abdominal cavity and is covered by the closely adhering peritoneal membrane, in which the mesovarium of each ovary originates.

Posteriorly the intestine is dorsally situated, and the mesentery is there so narrow that the intestine appears to be almost adherent to the peritoneum of the air bladder.

Huxley correctly described the anterior origin of the oviducal membrane at the posterior end of each ovary and the relative situation of each ovary, the right or smaller ovary being posterior to the left or larger ovary.

The oviducal membranes, as in the case of the salmonids, finally unite in a common channel above the intestine. Both of these oviducal membranes, when not containing ova, posteriorly, lie against the membrane of the air bladder which forms the roof of the so-called funnel.

The gravid ovaries practically fill all the space in the abdominal cavity not occupied by other viscera. Upon opening the fish from throat to vent along the median line of the belly and laying the lateral walls aside, at first glance there appears to be one single mass of eggs in front of which is the liver; posteriorly a small portion of the intestine may be visible. The greater portion of the egg mass is the anteriorly situated left ovary which extends from the liver to some distance beyond the base of the ventral fins (fig. 8 *a*). Closely juxtaposed to the posterior end of the left ovary is the right ovary (fig. 9 *b*) which extends nearly to the vent. The dividing line, which is often difficult to discern, beginning perhaps a little in advance of the ventral fins, extends obliquely from the right side (left as observed) backward to the left side (right as observed). Both ovaries are ventrally convex from side to side, and concave above, thus forming a broad, more or less triangular, continuous groove in which anteriorly the stomach lies. The intestine, at first above the stomach, finally lies in the grooves of the left and right ovaries. These grooves are formed by the left ovary curving over so that its so-called lower edge is in contact, or nearly so, with the dorsal surface of the abdominal cavity on the right side, and the left ovary curving in like manner in the reverse direction.

Except in shape and relative position the ovaries are much like those of the salmonids previously described. They are nearly covered by a very delicate membrane which is so thin that it is easily broken or rubbed off, so that one may be easily deceived into believing that there is no membrane and that the eggs are free in the abdominal cavity.

The mesovarium (fig. 9 *c*) arises near the lateral edge of the air bladder, and, in the case of the anterior ovary, its line of attachment gradually passes obliquely inward to its attachment to the intestine. The mesovarium of the posterior ovary has a proportionally longer intestinal attachment.

As in the Salmonidæ, the dorsal mesentery (fig. 10 *t*) ends some distance from the posterior end of the intestine (fig. 10 *w*), and the mesovarial membranes unite to form the floor of the common opening above the intestine. The outer edges continue attached to the lateral walls of the abdominal cavity (figs. 9 *g* and 10 *g*). Thus the mesovarian membranes, originating on the outer side of each ovary and deflecting to the abdominal walls, form the floors of the respective oviducts, while the peritoneum of the air bladder, the abdominal walls, and the mesentery form the other boundaries.

As in the case of the Salmonidæ, the portion of each ovary uninvested with adherent membrane consists of a narrow dorsal area which is tipped in against the mesovarium. In these passages, formed by the investing membranes, the ova pass backward into the oviducts. If they are set free into the abdominal cavity, there appears to be no conceivable way by which they can be extruded. The smelt appears to have no ventral mesentery, unless a close adhesion to the ventral or abdominal surface near the vent is such.

As previously stated, the gravid ovaries are situated one behind the other and almost entirely fill the abdominal cavity, save the comparatively small space occupied by other viscera. Before the ova of the left ovary have entered the oviduct, the gravid right ovary presses the left oviducal membrane (fig. 9 *g*) against the air bladder and left abdominal wall.

The ova of the right ovary ripen, enter the oviduct, and are deposited first. As the right ovary is emptied and its oviduct (fig. 10 *g*) is filled, the ova of the left ovary enter its oviduct and the empty and collapsed right ovary is compressed between the distended left oviduct and the right abdominal wall. The left ovary and its distended oviduct, together with the distended right oviduct, then have the appearance of a single mass of eggs, but, by careful manipulation, a longitudinal line of separation may be detected. As the right oviduct is emptied the left becomes entirely filled and with the remaining ova in the left ovary has the appearance of a single continuous ovary. Probably this was the condition which deceived Bloch, causing him to think that the smelt had but one ovary. When both ovaries are emptied and collapsed, the left is considerably anterior to the right and may have the appearance as described by Huxley; that is, a semioval plate, laminated on the outside and having a marginal membrane of about one-third its width.

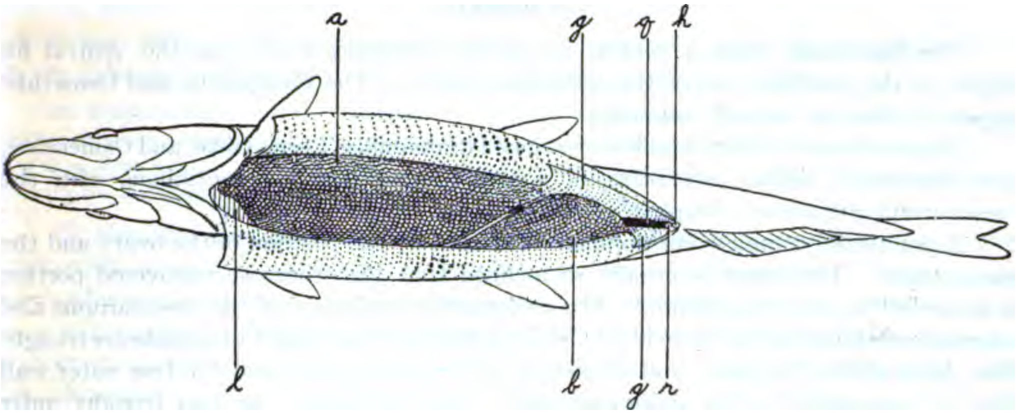

FIG. 8.—Semidiagrammatic drawing made by Walter H. Rich, from dissection by William C. Kendall. Specimen from Sebago Lake, Me. Ventral view of ovaries and oviducts of smelt (*Osmerus mordax*). *a*, Left or anterior ovary; *b*, right or posterior ovary; *g*, lateral expansions of mesovaria and ovarian membranes joining peritoneum of abdominal walls to form oviducts; *h*, genital pore; *l*, liver; *q*, intestine; *r*, anus.

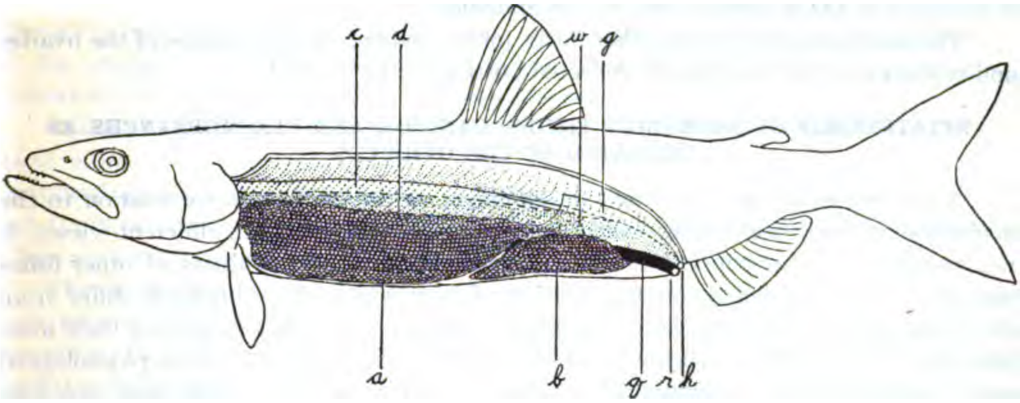

FIG. 9.—Left view of ovaries and membranes of same as fig. 8. *a*, Left ovary; *b*, left side of right ovary bending up on left side so that its lower portion is dorsally situated; *c*, left mesovarium; *d*, outer edge of ovarian membrane; *g*, posterior lateral expansion of mesovarium and ovarian membrane forming left oviduct; *h*, genital pore; *q*, intestine; *r*, anus; *w*, posterior end of intestinal mesentery with confluent mesovaria.

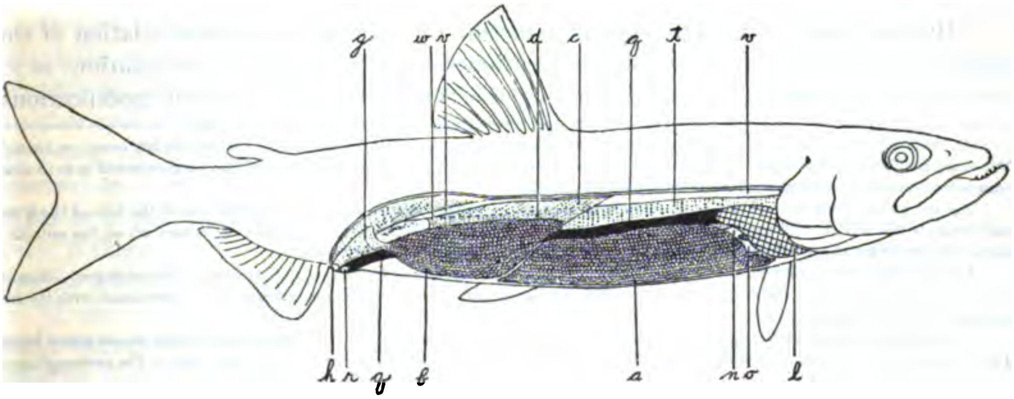

FIG. 10.—Right view of same as fig. 9. *a*, Left ovary bending up under stomach and intestine forming a groove in which the viscera extend; *b*, right ovary; *c*, mesovarium of right ovary; *d*, outer edge of ovarian membrane, between which and the mesovarium the egg surface not covered by membrane other than the mesovarium is situated; *g*, right posterior expansion of the mesovarium and ovarian membranes forming the short right oviducts or practically the right side of the common oviduct posterior to *w*; *h*, genital pore; *l*, liver; *n*, upper or cardiac arm of stomach; *o*, lower or pyloric arm of stomach; *q*, intestine; *r*, anus; *t*, intestinal mesentery; *v*, air bladder; *w*, posterior end of intestinal mesentery with confluent mesovaria.

SUMMARY.

The Salmonidæ have a ventral mesentery extending from near the ventral fin region to the posterior end of the abdominal cavity. The Coregonidæ and Osmeridæ appear to have no ventral mesentery.

The ovaries of the three families mentioned (Salmonidæ, Coregonidæ, and Osmeridæ), are structurally similar, consisting of a membranous covering continuous with the mesovarium and almost completely enveloping the ovigerous stroma.

A practically complete envelopment is formed by the position of the ovary and the mesovarium. The ovary is usually so inclined that the otherwise uncovered portion is protected by the mesovarium.[1] The prolongation backward of the mesovariums and ovarian investments form the oviducts, which in the Salmonidæ and Coregonidæ are trough-like, open above, the inner wall consisting of the mesovarium and the free outer wall (fig. 7 *f*) supported by the abdominal wall. Near the outlet, the two troughs unite into one above the intestine at the point of termination of the dorsal mesentery. At a short distance from the genital orifice each outer wall of the common channel is deflected and is attached to the respective wall of the abdomen.

The smelt differs from the other forms mentioned only in the position of the ovaries and in the extent of the lateraly deflected portion of the oviducts.

RELATIONSHIP OF SALMONOID FISHES, GANOIDS, AND ELASMOBRANCHS AS INDICATED BY THE OVIDUCTS.

A discussion of the origin and development of the oviduct in its relation to the nephridial system, concerning which morphologists still entertain different views, is not pertinent to this paper, but a brief consideration of the oviducts of other fishes may have some bearing upon the question of how widely the salmonoids differ from the other forms respecting these structures. Huxley wrote that, whatever their morphological nature, the arrangement of the membranes in the smelt in a physiological sense was, obviously, comparable to that of Fallopian tubes, and that everyone who was familiar with the anatomy of the female reproductive organs of the ganoids would at once perceive that these passages are the homologues of the oviducts of Acipenser, Polyodon, Polypterus, and Amia.

Huxley observed no difference in structure or essential anatomical relation of the oviducts of the smelt and the ganoids mentioned. In the structure and relations of its oviduct, he regarded Osmerus as forming the third term of a series of modifications, tending toward the separation of the ureteric from the oviducal ducts, two terms of which were presented by the ganoids, and the arrangement of the parts which obtain in the ordinary Salmonidæ a fourth term. Huxley stated as follows:

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[1] In two humpback salmon there appeared to be more or less free egg surface on the upper outer side of the left ovary, as though the ovary had been unduly stretched by the growing ova, and the surface usually inclined inward had been crowded so as to seem somewhat outward. The most marked instance was as follows:

The left ovary is about 250 mm. long, and about 45 mm. in vertical height near the posterior end of the lobe of the liver, extending to the outlet. The mesovarium is attached to the upper edge—the ovarian membrane comes up on the outside a little over one-third the width of ovary, making the exposed egg area comparatively wide.

About at the point of anterior attachment of the ventral mesentery, the ovary passes up to the top of the intestine. Then its vertical height is 25 mm. The end of the ovary within its almost completely infolding membrane lies in the trough with the free egg surface nearly dorsal.

The dorsal mesentery ends about 60 mm. from the posterior end of ovary. A little anterior to this, the mesovarium leaves the dorsal attachment and extends free on the inner side of the top of the ovary, lying in the trough (due to the prolongation of the ovary backward).

The right ovary is nearly 190 mm. long and 42 mm. wide, at about the anterior end of spleen. At this place is the only free egg space to be seen without tipping the ovary. This space is semioval in shape. These membranes are 14 mm. in narrowest place. The outer edge of membrane at posterior end runs diagonally across to mesentery and extends downward to form the side of the dorso-intestinal trough.

> The abortion of the oviducts, commenced in Osmerus, is completed in Salmo, and all that remains of the primitive arrangement is the fold described by Rathke and the so-called abdominal pore, which, it will be observed, is the homologue of half of the urogenital opening of the ganoids and has nothing to do with the abdominal pores of these fish and of the selachians.

He also says that, as is well known, Lepidosteus presents an example of a ganoid with oviducts like those of the higher Teleostei; in Osmerus, on the other hand, we have a teleostean with oviducts like those of the ordinary Ganoidei. It is tolerably obvious, he continues, that, therefore, the characters of the female reproductive organs can lend no support to any attempt to draw a sharp line of demarcation between the ganoids and the teleosteans.

Bridge (1904) distinguishes two types of genital ducts in fishes: (1) Those which are obviously derived from some part of the kidney system; and (2) those which are special ducts and appear to have no connection with kidney ducts. The elasmobranchs offer a typical example of the first, and the Teleostei afford an equally typical example of the other. Representatives of certain other orders, among which are Acipenser, Polyodon, and Amia (Amiatus), are regarded as more or less transitional.

Whatever may have been their embryological origin, it is quite clear that in the adult teleost the ovaries and oviducts have no relation to organs other than that of peritoneal attachment. These fishes, according to previously cited authorities, present two types of ovaries, free and closed, and three oviducal adaptations, closed peritoneal tubes, peritoneal funnels, and no oviducts at all except the ovipore.

The closed ovary is said to develop in two ways from the genital ridge: (1) By the upturning and attachment above of the lower edge of the genital ridge, thus infolding the genital cells; and (2) by the formation of a groove on the surface of the ridge, the genital cells becoming infolded by the conjunction of the two edges of the groove.

The so-called free ovary, accordingly, was supposed to be formed by the genital cells developing on the outer side of the ridge and the lower edge folding up only slightly or not at all.

In each instance of closed ovary the closed oviduct is formed by a backward extension of the ovarian peritoneal membrane, the process of its formation being somewhat different, according to whether the ovary is of the upturning or groove development. In either case an extension backward of the mesovarium is involved. In the case of the free ovary, the oviduct, if any, is developed wholly from the backward extension of the mesovarium. In the case of the closed ovary, according to Goodrich (1909), the oviduct begins as a parovarial or endovarial channel blind in front. In the case of the free ovary, if there is any oviduct, it is said to begin as the wide mouth of a funnel near the posterior end of the ovary or at some distance behind it.

In the case of the ganoids previously mentioned, there is obviously a veritable funnel formed by the folding of the peritoneal membrane on itself, which is well exemplified by that of Amia (Amiatus), as shown by Huxley.

According to the same authority, the smelt differs from the ganoids in having the outer edge of the peritoneal fold attached to the abdominal wall, yet it is still called a "funnel" and considered homologous with the oviducal funnels of ganoids.

There is this difference between the oviducal membrane of the smelt and the funnel of the ganoids mentioned, that in the smelt the membrane turns outward to become attached to the abdominal wall (fig. 8 *g*), while in the other form it folds inward and is attached to the mesovarial membrane (fig. 11). In the latter a funnel is formed; in the former, only a half-funnel, which is not a homologue of the ganoidean funnels, but is homologous with the oviducts of other Isospondyli, even (some at least) of those with closed oviducts. Any phylogenetic significance of the smelt oviduct then would appear to pertain only to teleosts and to have no relation to the ganoids.

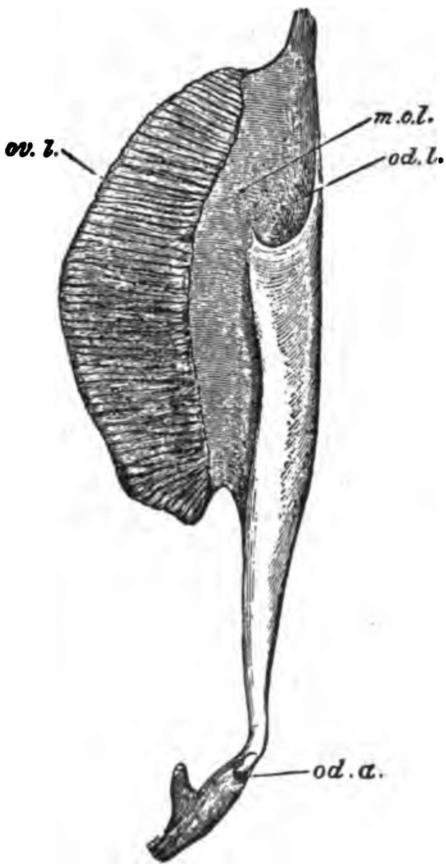

FIG. 11.—Left ovary and oviduct of bowfin (*Amiatus calvus*), after Huxley. ×643. *ov.l.*, left ovary; *m.o.l.*, left mesovarium; *od. l.*, left oviduct; *od. a.*, opening of oviduct into the bladder.

The Isospondyli comprise forms which are stated to have closed ovaries and true oviducts as well as those which have free ovaries with funnel-like oviducts or only vestigial oviducts.

Besides the previously mentioned species, specimens of *Pomolobus pseudoharengus*, *P. mediocris*, *Dorosoma cepedianum*, and *Hyodon tergisus* have been carefully examined. The following two examples will serve to show that the Isospondyli, other than Salmonidæ, as represented by the specimens examined, are not radically different in their general structure from the Salmonidæ, but considerably different from other orders having closed ovaries.

The clupeoids are supposed to have closed ovaries and oviducts. In the alewife (*Pomolobus pseudoharengus*), the ovary of a large adult, taken July 4, therefore some time after the breeding season, is long and narrow, extending well back in the abdominal cavity. The mesovarium is narrow, the ovary lying close to the air bladder. Anteriorly the line of attachment of the outer edge of the enveloping membrane is close to the junction of the inner attachment of the mesovarium to the ovary, along the outer side of the air bladder, and there is a projection forward of the ovary, which is completely inclosed in membrane with no air-bladder attachment of the mesovarium. Posteriorly the lines of attachment diverge slightly, so that the inner line continues along the air bladder, but the outer one becomes attached nearer to the lateral abdominal wall at the side of the air bladder. The mesovarium is so narrow that it is scarcely perceptible except as a fold lying in the outside of the ovary, but the membranous attachment is wider and free from ovigerous laminæ, leaving a noticeable space of free eggs; that is, without other covering than the peritoneum of the air bladder. This free-ova portion constitutes the beginning of the oviduct within and on one side of the ovary. The remainder of the oviduct consists of the extension of the mesovarium and outer attached edge of the ovarium membrane forming a channel with a very narrow roof of dorsal peritoneum. The two oviducts unite near the outlet. This alewife has a ventral mesentery of about the same relative extent as in the salmonids.

The hyodons are stated (Jordan and Evermann, 1896, p. 412) to have no oviducts, the eggs falling into the abdominal cavity before extrusion. An example of *Hyodon tergisus* in breeding condition showed that the ovaries are completely inclosed in membrane which, continuing from the mesovarium junction with the ovary, passes down its inner surfaces and up over the outer surface and upper edge, then downward again on the inner surface to the mesovarial attachment. The fusion of the outer edge of the ovarian covering with the mesovarium at its junction with the ovary appears to be complete as far back as the common opening in the dorsal mesentery. In this specimen the remainder of its backward extent seems to be still attached by fascialike, adhesive membrane similar to the adhesions of the viscera in general to the abdominal wall and to each other. At the termination of the mesentery posteriorly in the common opening an interovarian channel is formed by the continuation of the ovarian membranes. The membranes of the inner surface of each ovary fuse along the median longitudinal line of the upper surface of the intestine, forming the floor of a common oviducal channel, the outer sides of which are formed by the ovarian membranes of each ovary, beginning on the inner surface as a projecting fold. At this point the intestine and canal somewhat abruptly turn downward to the outlet. Another mesovariumlike membrane on each side begins forward, originating close to the mesovarium, and is attached to the upper surface of the ovary. It appears to continue backward beyond where the dorsal attachment of the true mesovarium ends and, by adhesion to the outer edge of the oviducal canal on each side, respectively, forms a closed oviduct. Excepting in this secondary membrane, this oviducal structure is very similar to that which has been described in connection with the Salmonidæ.

Since the intestine, with the superimposed oviducal canal, for the most of its extent is dorsally situated, it is quite evident that any ova falling into the abdominal cavity can not be extruded.

RELATION OF THE ANATOMICAL FACTS TO FISH-CULTURAL PRACTICES.

Boulenger (1904, p. 568) says of the Salmonidæ:

> The large size of the eggs, their lack of adhesiveness, and the fact that the ova fall into the abdominal cavity, out of which they may be easily squeezed, renders artificial impregnation particularly easy and the species of Salmo have always occupied the first place in the annals of fish culture.

The error of this statement has been shown in the foregoing pages. It has been seen that the mature ovary is inclosed in a delicate membrane, which is a continuation of the peritoneal fold called the mesovarium. From the posterior end of each ovary an open membranous trough extends inward and backward to the median line of the upper surface of the intestine at the posterior termination of the dorsal mesentery, whence, by a fusion with each other mesially, a single oviducal trough, open above, which conveys the ova to the genital pore, is formed on the upper surface of the intestine.

Inasmuch as the ova do not naturally fall into the abdominal cavity and can not be extruded if they are displaced into it, it follows that their adventitious presence there can not be of advantage to the fish. Fish-cultural methods afford several means of displacing eggs into the abdominal cavity. There is abundant evidence that present fish-cultural methods cause such displacements. They may be occasioned by dipping the fish head first into a scoop net, which causes considerable flopping by the fish; or by grasping the fish by the tail and holding her head downward until her struggles cease. If the fish is ripe, or partly ripe, the mass of eggs sags visibly toward the head, and it would seem inevitable that any free eggs would settle into the forward end of the abdominal cavity outside of the ova-containing membrane. It is, however, after the stripping process has begun that the danger of displacement is greatest, and particularly after some eggs have been expressed and the tense condition of the supporting abdominal wall is relaxed. It is largely due to displacement that the repeated stripping process fails to secure all of the ripe eggs, and even should the fish subsequently emit retained eggs, it is manifestly impossible for her to rid herself of displaced eggs.

Another disadvantage from which the fish may suffer is rupture of the membranes and injury to the ovaries by forcible pressure, so that the eggs falling into the abdominal cavity are not secured. The ovary thus injured may not recover its natural function and may thereby become sterile.

I have dissected various salmonids which have had deformed or distorted ovaries and others with postnuptial reduced ovaries containing hardened eggs of the previous or some preceding season, and have observed several instances of rainbow trout which had been stripped some months previously, containing masses of collapsed eggs adhering to each other, the viscera and abdominal walls, and others more recently stripped, in which the ovaries still contained eggs, in follicles, more or less crushed, and in one instance of which the posterior end of the ovary still containing eggs had been broken off and was loose in the abdominal cavity. Several samples of ruptured ovaries have been observed. In one example of landlocked salmon, several eggs had been pressed into the under side of the lobe of the liver so that they showed through on the outside. These facts can be ascribed to nothing except forcible attempts to strip the fish.

Some of these fish were artificially reared trout from a hatchery whence had come a complaint that the trout were yielding fewer eggs than the normal yield, and concerning which the suggestion was offered that the deterioration was due to inbreeding.

It is a common practice to begin the stripping pressure well forward and to repeat the movement until all eggs possible have been squeezed out, the last frequently being accompanied by fecal matter, mucus, and blood, This process is not only liable to injure the ovaries and membranes, but to express unripe eggs, impossible of fertilization. In fact, all of the eggs are never secured and some are retained and apparently are not subsequently naturally extruded.

In A Manual of Fish-Culture, Charles G. Atkins (1900, p. 35) thus describes the process of taking eggs from the Atlantic salmon:

> The spawntaker clad in waterproof clothing and wearing woolen mittens, sits on a stool or box, and on a box in front of him is a clean tin pan holding about 10 quarts, which has been rinsed and emptied, but not wiped out. A female salmon is dipped up from one of the floating pens and brought to the operator, who seizes her by the tail with the right hand and holds her up, head downward. If unripe, the fish is returned to the pens; if ripe, the spawn will be loose and soft and will run down toward the head, leaving the region of the vent loose and flabby, and the operator, retaining his hold of the tail with his right hand, places the head of the fish under his left arm with the back uppermost, the head highest, and the vent immediately over the pan. At first the fish generally struggles violently and no spawn will flow; but as soon as she yields, the eggs flow in a continuous stream rattling sometimes

> with great force against the bottom of the pan. Shortly the flow slackens and must be encouraged and forced by pressing and stroking the abdomen with the left hand. It is better to use the face of the palm or the edge of the hand rather than pinch between the thumb and fingers; the latter action, especially when working down near the vent, is apt to rupture some of the minor blood vessels, with the result of internal bleeding, and it is better to leave some of the eggs behind to be taken another day than to run the risk of such rupture.

In the same publication, George A. Seagle (1900, p. 66) describes a somewhat more careful method of taking eggs from the rainbow trout as follows:

> In taking spawn the manipulation of the fish without injury is a very delicate and exacting task, full knowledge of which can only be acquired by experience, as it is difficult to squeeze the spawn from the fish without injuring or even killing it. In taking hold of the fish in the spawning tub the operator catches it by the head with the right hand, the back of the hand being up, and at the same time slips the lefthand under the fish and grasps it near the tail, between the anal and caudal fins. If the fish struggles it must be held firmly, but gently, until it becomes quiet, and when held in the right position it will struggle only for a moment. A large fish may he held with its head under the right arm.
>
> When the struggle is over the right hand is passed down the abdomen of the fish until a point midway between the pectoral and ventral fins is reached; then, with the thumb and index finger, the abdomen is pressed gently, and at the same time the hand is slipped toward the vent. If the eggs are ready to be taken they will come freely and easily, and if they do not the fish is put back in the pond until ready to spawn. If the eggs come freely from the first pressure the operation is repeated, beginning at or near the ventral fin.
>
> After the first pressure has been given, by holding the head of the fish higher than the tail, all of the eggs that have fallen from the ovaries and are ready to be expressed will fall into the abdomen, near the vent, so that it will not be necessary to press the fish again over its vital parts, the eggs having left that portion of the body. All of the eggs that have fallen into the abdomen below the ventral fin can be easily ejected without danger of injury to the fish, caused by unnecessary pressure over its important organs after the eggs have left that part of the body. If these directions are judiciously and carefully followed, but little, if any, damage will result; and, as an illustration, it may be mentioned that fish have been kept for 14 years and their full quota of eggs extracted each season during the egg-producing term, which is normally from 10 to 12 years. The male fish is to be treated very much in the same manner as the female, except the milt must not be forced out, only that which comes freely being taken.

At the thirteenth annual meeting of the American Fish Cultural Society, Charles G. Atkins presented some notes on the landlocked salmon, regarding which, among other things, he said:

> Among the migratory salmon of the Penobscot, ovarian disease is rare; but with the landlocked salmon of the Schoodic Lakes it is very common. In 1883, by careful observation, we learned that 18 per cent of the female fish were affected with some disease of the ovaries, resulting in defects of the eggs which were apparent to the eye, in some instances involving the entire litter, but generally a very small number of eggs. The phenomenon was observed before artificial breeding began at Grand Lake Stream, and does not appear to be influenced thereby.

Atkins does not state under what circumstances or conditions the phenomenon was previously observed, but it is, perhaps, significant that following the adoption of the gradual stripping process at Grand Lake Stream there were no further reports of "ovarian trouble" or defective eggs among the salmon.

These facts indicate that in the case of those salmonoids which normally survive the season of reproduction, all care possible should be exercised in the process of manipulation for the purposes of artificial propagation.

The fish should be gently handled and at no time should be permitted to hang and struggle head downward. Inasmuch as the fish does not naturally emit the eggs at one time, in stripping a fish this fact should be borne in mind, and no forcible attempt should be made to express more than those eggs which easily flow under gentle pressure. It may take several operations to secure all of the eggs, and as the eggs begin to ripen in the posterior part of the ovary, to obtain them it is not necessary to squeeze the whole length of the abdomen. In fact, it is liable to injure the eggs or rupture the ovarian membrane to do so. Experiments indicated that by the usual method of stripping a large percentage of the eggs are obtained in the first operation. The question, therefore, arises whether the number of good eggs obtained would be reduced by a gentler operation and whether a second operation is necessary. In any event it would seem to be a more rational procedure to follow nature and first remove the eggs in the posterior end of the fish, using no more force than gentle pressure near the vent, with a movement toward it. If eggs do not flow at first, repeated, short, gentle strokes may cause them to, if they are ready to be deposited. Some egg takers hold the fish belly up at an angle which will permit the eggs to fall into the pan for receiving the eggs. It would seem to be more in accordance with nature if the fish were held belly down thus permitting the eggs to flow or roll along the oviduct toward the vent, as others are emitted. The flow may be aided by gentle stripping motions repeated each time a little further forward, not going further than the region of the middle of the ventral fins. When the eggs cease to flow under gentle stripping pressure the operation should cease. Possibly not as many eggs would be obtained by this method as by the usual forceful method, but by operating only once or twice with due care, the danger of both external and internal injuries is lessened, and the breeder is saved, providing retained eggs are not harmful. This latter point remains to be ascertained.

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FURTHER LIMNOLOGICAL OBSERVATIONS ON THE FINGER LAKES OF NEW YORK

By Edward A. Birge and Chancey Juday

From BULLETIN OF THE BUREAU OF FISHERIES, Vol. XXXVII, 1919–20

Document No. 905 *Issued October 8, 1921*

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WASHINGTON : GOVERNMENT PRINTING OFFICE : 1921

CONTENTS.

Page.

Introduction 211

Temperatures and heat budgets 211

  Surface and bottom temperatures 212

  Thermal regions 213

  Summer heat income 215

Distribution of heat 218

  Direct work 219

  Distributed work 221

  Subtraction curves 221

  Heat and work as measured at depth 222

Absorption of sun's energy 223

Work of the sun in distributing heat 232

Plankton 235

  Methods 235

  Net plankton 236

    Phytoplankton 236

    Zooplankton 236

  Nannoplankton 241

  Plankton tables 243

Bottom fauna 250

Literature cited 252

FURTHER LIMNOLOGICAL OBSERVATIONS ON THE FINGER LAKES OF NEW YORK.

By EDWARD A. BIRGE and CHANCEY JUDAY,
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INTRODUCTION.

In 1910 and 1911 the U. S. Bureau of Fisheries enabled the authors of the present paper to spend some weeks in the study of the Finger Lakes of New York. The results of this work were published in the Bulletin of this Bureau for 1912 (Birge and Juday, 1914). In this expedition there were applied to the study of the New York lakes methods that had already been tried on the lakes of Wisconsin, which are much smaller and shallower than those of New York. The resulting report dealt with the hydrography of the lakes, their temperatures and heat budgets, their content of dissolved gases, and their net plankton. Since that study was made, the Wisconsin survey has increased the scope of its observations on lakes. In particular there has been devised and used extensively a new instrument, the pyrlimnometer, designed for measuring the transmission of the sun's radiation through the water of a lake; numerous determinations of the weight of the individual members of the net plankton have been made; an elaborate study of the nannoplankton, both numerical and quantitative, has been completed; and it is now possible to make a rough correlation between count and weight of both net plankton and nannoplankton.

The Bureau of Fisheries authorized a second expedition to the New York lakes in July and August of 1918, in order to apply these newer methods to them. The following paper reports the results of the observations.

The authors are indebted to Hobart College, Geneva, for the free use of its laboratories during their stay on the lakes, and to Prof. E. H. Eaton, of the same college, for unwearied assistance in their work. Much of the success which was reached was due to this aid. All recorded series of temperatures between 1911 and 1918 were taken by Prof. Eaton, as also were those taken after August 1, 1918.

This report comes from both of its authors, as was the case with their former paper on the same subject. Mr. Juday, however, has prepared the part which deals with the plankton and Mr. Birge that which relates to temperatures and transmission of radiation.

TEMPERATURES AND HEAT BUDGETS.

The temperatures of the Finger Lakes were discussed in our former paper (Birge and Juday, 1914, pp. 546–575), and it is unnecessary to repeat what was said there. Additional observations have been made and the discussion can be enlarged, therefore, at certain points.

Table 1 shows the dates at which series of temperatures have been taken for use in computing the summer heat income. A five-year mean of August temperatures may be obtained for Canandaigua and Cayuga Lakes and a four-year mean for Seneca Lake. Additional observations are not likely to make essential changes in the results thus obtained.

SURFACE AND BOTTOM TEMPERATURES.

Observations of the surface in August and early September show in Canandaigua Lake a mean of 21.4° C., ranging from 20.7 to 21.7°; in Cayuga Lake the mean is 21.1°, ranging from 19.8 to 22.6°; in Seneca Lake, 20.4°, ranging from 20.0 to 21.1°. These must not be taken as the maximum surface temperatures, which undoubtedly are likely to come earlier in the season. Seneca Lake was visited on July 24, 1918, in the afternoon of a clear, hot day and at the close of a hot and windless period. The surface temperature in water 40 m. deep was 25.0° C. A heavy shower with violent squalls occurred later in the afternoon. The surface temperature on July 25 was 20.8° and there was a marked rise of temperature above that of the 24th at all depths between 5 and 30 m.

TABLE 1.—DATES OF TEMPERATURE SERIES: SURFACE, BOTTOM, AND MEAN TEMPERATURES.

Lake and date.	Surface.	Bottom.	Mean.
CANANDAIGUA LAKE.	°C.	°C.	°C.
Aug. 20, 1910	21.7	5.4	11.05
Sept. 4, 1911	20.7	4.3	10.02
Aug. 27, 1914	21.6	4.5	10.11
Aug. 31, 1916	21.6	5.0	11.57
July 27, 1918	23.1	5.1	11.91
Sept. 1, 1918	21.5	5.0	11.42
Mean	21.4	4.8	10.95
CAYUGA LAKE.			
Aug. 11, 1910	19.8	4.3	9.24
Sept. 2, 1911	20.0	4.1	8.93
Sept. 4, 1914	21.4	4.1	9.65
CAYUGA LAKE—continued.	°C.	°C.	°C.
Aug. 16, 1917	22.6	4.3	9.44
Aug. 30, 1918	22.0	4.2	9.66
Mean	21.1	4.2	9.43
SENECA LAKE.			
Aug. 3, 1910	20.2	4.2	7.71
Sept. 1, 1911	20.0	4.0	7.34
Sept. 5, 1914	21.1	4.0	8.27
Aug. 29, 1918	20.8	4.0	8.07
Mean	20.4	4.05	7.84

Bottom temperatures average 4.8° C. in Canandaigua Lake (84 m. deep), ranging from 4.3 to 5.4°; in Cayuga Lake (133 m.) they average 4.2° with a range from 4.1 to 4.3°; in Seneca Lake (188 m.) the mean is 4.05° and the range from 4.0 to 4.2°. The reading was 4.0° in three of the four series.

In most of these cases the observations were made with a Negretti and Zambra deep-sea thermometer divided to 0.5°. Such an instrument gives approximate but not very exact results. In 1918 the attempt was made to ascertain whether the water of Seneca Lake might not be below 4.0° C. at the bottom. The temperature of maximum density is lowered by pressure, as pointed out by Hamberg (1911, pp. 306–312). Since the depth of Seneca Lake is 188 m. the pressure at the bottom is about 19 atmospheres, and maximum density would be reached between 3.3 and 3.4°.

A special thermometer was used, ranging from −2.0 to +14.0° and divided to 0.1°. This instrument read exactly 4.1° when at the temperature of the surface water, 19.3°. Correction for the expansion of the mercury shows that the true temperature at the bottom was 3.88° and, therefore, below 4.0°, though decidedly above the temperature of maximum density for the depth. Hamberg (loc. cit.) quotes examples of similar temperatures from Lakes Ladoga and Mjösen. It is worth noting that the temperature in both these lakes at the depth of 190 m. was between 3.8 and 3.9°. The observations of Huitfeld-Kaas (1905, p. 4) in Mjösen give temperatures at 200 m. which rise as high as 4.1° in November and as low as 3.65 or 3.75° in April and May. At the bottom, 400 m. or more, 3.60 and 3.75° were found. At this depth the temperature of maximum density is slightly above 3.3°.

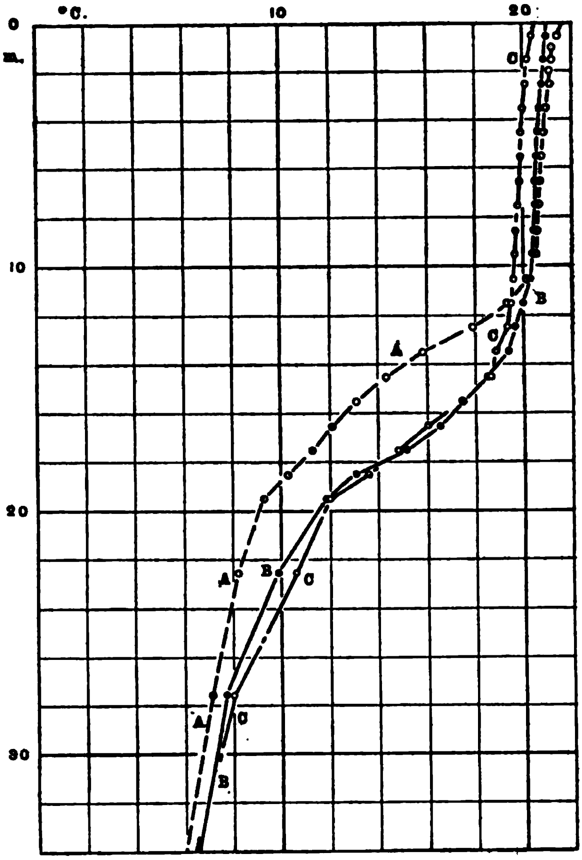

Fig. 1.—Curves of mean temperature to 34 m. depth. *A*, Canandaigua Lake; *B*, Cayuga Lake; *C*, Seneca Lake. (See Table 1, p. 212.)

It is very probable that the temperature of Seneca Lake, recorded in 1910 as 4.2°, was really close to 4.0°, and that all readings of 4.0° at the bottom indicate temperatures as low as 3.8 or 3.9°. It is not worth while, however, to apply an estimated correction to these readings. There is no reason to believe that the bottom temperature of Cayuga Lake is below 4.0° in late summer.

THERMAL REGIONS.

Table 2 shows the thermal regions of the several lakes. The epilimnion of Canandaigua Lake was 11 or 12 m. thick; the thermocline was 4 to 8 m. thick, averaging 6 m. In Cayuga Lake the epilimnion was 13 to 15 m. thick and the thermocline 4 to 5 m. thick.

There was more variation in Seneca Lake. The epilimnion was 15 to 19 m. thick and the thermocline 4 to 6 m. On August 1, 1918, the epilimnion at Hector Point was only 10 m. thick; on August 29, at Kashong, it was determined at 20 m. But since Kashong is near the north end of the lake and the readings were taken on the day following a hard south wind, the epilimnion was no doubt thicker there than observations at the center of the lake would have shown. In computing gains of heat, therefore, the thickness of the epilimnion for 1918 was taken as 15 m.

On July 24, 1918, at the north end of the lake in 40 m. of water the epilimnion was only 7 m. thick. This was at the end of nine days of hot and calm weather and is an exceptional condition. The thickness of the epilimnion rapidly increased to 14 or 15 m. in the course of the following week and was subject to considerable fluctuations.

TABLE 2.—DISTRIBUTION OF SUMMER HEAT INCOME TO THERMAL REGIONS OF LAKES.

[NOTE.—Mean is derived from mean temperatures. Extent=vertical thickness of region in meters; R. T.=reduced thickness of region, i. e., the thickness in meters of the region when reduced to the area of the surface of the lake. It is computed by dividing the volume of the stratum expressed in meters by the area of the surface of the lake expressed in square meters; T=gain of heat above 4.0°, i. e., the summer heat income expressed in degrees centigrade; Cal.=gram calories per square centimeter of lake surface; P. ct.=per cent.]

CANANDAIGUA LAKE.

Thermal region.	1910					1911				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–12	10.0	16.8	16,800	61.8	0–12	10.0	15.5	15,500	66.4
Thermocline	12–20	5.6	9.3	5,200	19.1	12–20	5.6	9.2	5,200	22.0
Hypolimnion	20–84	23.1	2.73	5,200	19.1	20–84	23.1	1.04	2,400	11.6
Mean or total	....	38.7	7.07	27,200	....	....	38.7	5.99	23,200	....

Thermal region.	1914					1916				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–11	9.34	21.0	15,830	58.6	0–12	10.8	21.2	17,420	59.3
Thermocline	11–18	5.01	14.0	5,010	18.6	12–20	5.64	13.3	5,270	17.9
Hypolimnion	18–84	24.45	6.5	6,160	22.8	20–84	23.08	6.9	6,680	22.7
Mean or total	....	38.8	10.96	27,000	....	....	39.52	11.57	29,370	....

Thermal region.	1918					Mean.				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–11	9.34	20.7	15,610	54.3	0–11	9.34	20.8	15,660	58.0
Thermocline	11–15	2.91	16.2	3,560	12.4	11–17	7.18	15.9	4,970	18.4
Hypolimnion	15–84	26.25	7.7	9,600	33.3	17–84	25.82	16.5	6,350	23.6
Mean or total	....	38.5	11.42	28,770	....	....	42.34	10.95	26,980	....

CAYUGA LAKE.

Thermal region.	1910					1911				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–15	11.8	15.5	18,300	64.2	0–16	12.5	15.2	19,000	71.1
Thermocline	15–22	4.62	10.3	4,800	16.9	16–21	3.3	9.2	3,300	12.4
Hypolimnion	22–133	38.3	1.41	5,400	18.9	21–133	38.7	1.14	4,400	16.5
Mean or total	....	54.72	5.26	28,500	....	....	54.5	4.94	26,700	....

Thermal region.	1914					1917				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–15	11.97	21.2	20,624	66.8	0–13	10.56	21.0	17,977	60.5
Thermocline	15–20	3.35	16.7	4,266	13.8	13–17	2.76	15.6	3,201	10.8
Hypolimnion	20–133	39.27	5.5	5,980	19.4	17–133	14.29	6.1	8,542	28.8
Mean or total	....	54.59	9.65	30,870	....	....	27.61	9.44	29,720	....

Thermal region.	1918					Mean.				
	Extent.	R. T.	T.	Cal.	P. ct	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–15	11.97	20.4	19,734	63.9	0–15	11.97	20.3	19,538	66.2
Thermocline	15–19	2.70	14.0	2,716	8.8	15–20	3.35	14.9	3,643	12.4
Hypolimnion	19–133	39.94	6.1	8,460	27.3	20–133	39.27	5.6	6,309	21.4
Mean or total	....	54.61	9.66	30,910	....	....	54.59	9.40	29,480	....

TABLE 2.—DISTRIBUTION OF SUMMER HEAT INCOME TO THERMAL REGIONS OF LAKES—Continued.

SENECA LAKE.

Thermal region.	1910					1911				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–12	11.5	15.4	17,700	53.8	0–15	13.8	15.4	21,200	71.5
Thermocline	12–20	6.2	10.2	6,400	19.5	15–22	6.0	8.6	5,200	17.5
Hypolimnion	20–188	70.9	1.21	8,800	21.7	22–188	68.8	0.47	3,300	11.0
Mean or total	....	88.6	3.71	32,900	....	....	88.6	3.35	29,700	....

Thermal region.	1914					1918				
	Extent.	R. T.	T.	Cal.	P. ct.	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–19	16.92	20.0	27,000	71.2	0–15	13.60	20.0	22,420	62.2
Thermocline	19–25	4.83	13.9	4,780	12.6	15–19	3.32	14.6	3,510	9.8
Hypolimnion	25–188	66.85	4.9	6,090	16.2	19–188	71.68	5.4	10,030	27.9
Mean or total	....	88.6	8.27	37,870	....	....	88.6	8.07	36,060	....

Thermal region.	Mean.				
	Extent.	R. T.	T.	Cal.	P. ct.
Epilimnion	0–15	13.60	19.8	21,410	63.0
Thermocline	15–20	4.13	14.8	4,450	13.1
Hypolimnion	20–188	70.87	5.2	8,160	24.0
Mean or total	....	88.6	7.84	34,020	....

SUMMER HEAT INCOME.

The summer heat income represents the gains in heat of the water of the lake above the temperature of 4°. This notion was put forward in our paper on the New York Lakes (Birge and Juday, 1914, p. 562) under the name of "wind-distributed heat." In the following year (1915, p. 167) I proposed the name "summer heat income" for the same gains of heat, preferring a term which does not imply any theory as to the method of distributing such heat. For reasons discussed in the same paper (1915, p. 186) the summer heat income of lakes can be used as an index of their heat exchanges in much the same way as the annual heat budget. The heat income, like the heat budget, is stated in gram calories per square centimeter of lake surface. For the sake of brevity it is ordinarily stated as so many calories without adding in every case the qualifying terms. The whole question of heat budgets and the methods of computing them is discussed in the paper already referred to (Birge, 1915).

Table 2 shows the summer heat income of the three lakes concerned. Canandaigua Lake shows a mean income of nearly 27,000 cal./cm.^{2}, ranging from 23,000 to more than 29,000 cal. Cayuga Lake has an income of about 29,500 cal., ranging from less than 27,000 to nearly 31,000 cal. The income of Seneca Lake is about 34,000 cal., ranging from less than 30,000 to nearly 38,000 cal. The smaller income of Canandaigua Lake is mainly due to the thinner epilimnion, which, in turn, is due to the smaller size of the lake and to the protection from wind afforded by its high shores. So far as area goes, Cayuga Lake is as well off as Seneca and its depth is ample to secure as large an income. But while the epilimnion in both lakes is 15 m. thick, its reduced thickness is nearly 12 per cent less in Cayuga Lake than in Seneca. This fact is due to the large extent of shallow water at the north end of the lake, which causes a corresponding reduction in the amount of heat as stated in terms of units of surface area. The upper 20 m. of these lakes contains 75 to 80 per cent of the total quantity of heat, and the reduced thickness of this stratum in Cayuga Lake is nearly 14 per cent less than in Seneca Lake. (See Table 3.) The slightly higher temperature of the stratum in Cayuga Lake is not great enough to compensate for this difference in thickness (cf. Birge and Juday, 1914, p. 574).

A longer series of years would undoubtedly change the figures stated above. But it is not probable that such a series would greatly alter them or that it would change the general relations of the heat income of the several lakes to each other. The smaller lake has the smaller income, largely because of its thinner epilimnion. Cayuga Lake has less heat than Seneca, largely because of the smaller ratio between maximum and mean depth. The differences are not so great but that the series of budgets overlap, the largest heat income of Canandaigua being larger than the smallest of Cayuga, and Cayuga's series overlapping in a similar way that of Seneca. The largest heat income in the series is that of Seneca in 1914, nearly 38,000 cal.

Table 2 also shows the distribution of heat to the three thermal regions of the lakes. The epilimnion contains about 60 per cent of the summer heat income, ranging from 53 to more than 70 per cent. This stratum, together with its thermal dependency, the thermocline, contains from 70 to nearly 90 per cent of the heat. Thus in Seneca Lake, which may be nearly 200 m. deep, a surface stratum occupying little more than the upper one-tenth of the depth contains from three-fourths to nine-tenths of the heat accumulated from the sun during the season.

Table 3 shows the distribution of the summer heat income by 10 m. intervals. It shows the same facts as Table 2 but in another form. It makes especially clear the small amount of heat which can be carried to considerable depths. In Canandaigua Lake, for example, the total quantity of heat transmitted below 50 m. during the season does not exceed the quantity delivered to the surface in one summer day; and even in the much larger and deeper Seneca Lake it does not exceed two days' supply.

TABLE 3.—DISTRIBUTION OF TEMPERATURES AND OF CALORIES OF SUMMER HEAT INCOME.

[NOTE.—R. T.=reduced thickness of stratum in meters; T.= temperature in degrees centigrade; Cal. =calories of summer heat income, i. e., gain of heat above 4°; P. ct.=per cent of heat income in stratum.]

CANANDAIGUA LAKE.

Depth in meters.	R. T.	1910			1911			1914		
		T.	Cal.	P. ct.	T.	Cal.	P. ct.	T.	Cal.	P. ct.
0-10	8.56	21.2	14,720	53.3	19.9	13,610	58.2	21.1	14,640	56.3
10-20	7.16	14.3	7,370	27.0	14.2	7,300	31.5	13.6	6,870	26.4
20-30	6.43	7.4	2,190	8.0	6.1	1,350	5.6	7.4	2,190	8.4
30-40	5.71	6.2	1,260	4.7	4.9	510	2.4	6.3	1,310	5.0
40-50	4.88	5.8	880	3.3	4.6	290	1.2	5.4	680	2.6
50-60	3.65	5.6	580	2.3	4.5	180	.8	4.8	290	1.1
60-70	1.90	5.5	280	1.1	4.35	70	.3	4.6	110	.4
70-84	.53	5.4	70	.3	4.3	20	....	4.5	20	.1
	....	11.05	27,350	100.0	10.02	23,330	100.0	10.71	26,110	100.3

Depth in meters.	R. T.	1916			1918			Mean.		
		T.	Cal.	P. ct.	T.	Cal.	P. ct.	T.	Cal.	P. ct.
0-10	8.56	21.4	14,890	50.7	20.8	14,380	50.0	20.9	14,450	53.5
10-20	7.16	14.9	7,800	26.6	14.9	7,800	27.1	14.4	7,430	27.5
20-30	6.43	8.6	3,420	11.6	8.9	3,150	11.0	7.8	2,460	9.1
30-40	5.71	6.6	1,480	5.0	6.8	1,600	5.6	6.1	1,230	4.6
40-50	4.88	5.9	930	3.2	5.9	930	3.2	5.5	740	2.7
50-60	3.65	5.5	550	1.9	5.6	570	2.0	5.2	430	1.6
60-70	1.90	5.3	250	.8	5.4	270	1.0	5.1	200	.7
70-84	.53	5.0	50	.2	5.3	70	.2	4.8	40	.2
	....	11.57	29,370	100.0	11.42	28,770	100.1	10.95	26,980	99.9

TABLE 3.—DISTRIBUTION OF TEMPERATURES AND OF CALORIES OF SUMMER HEAT INCOME—Con.

CAYUGA LAKE.

Depth in meters.	R. T.	1910			1911			1914		
		T.	Cal.	P. ct.	T.	Cal.	P. ct.	T.	Cal.	P. ct.
0-10	8.42	19.2	12,800	44.8	19.9	13,400	40.8	21.3	14,600	47.3
10-20	6.88	17.7	9,400	32.9	17.1	9,000	33.5	18.8	10,200	33.0
20-30	6.27	8.8	3,000	10.5	8.2	2,600	9.7	9.6	3,500	11.3
30-40	5.79	6.4	1,400	4.9	5.6	900	3.4	6.2	1,300	4.2
40-50	5.12	5.4	700	2.4	4.7	350	1.3	5.2	600	1.9
50-60	4.52	4.9	400	1.4	4.4	180	.7	4.6	290	.9
60-70	4.03	4.6	250	.9	4.4	140	.5	4.4	160	.5
70-80	3.60	4.5	190	.6	4.3	130	.5	4.3	90	.3
80-100	5.89	4.5	290	1.0	4.2	120	.4	4.1	90	.3
100-133	4.09	4.4	170	.6	4.2	80	.3	4.1	40	.1
	54.61	9.24	28,600	....	8.93	26,900	....	9.65	30,870	....

Depth in meters.	R. T.	1917			1918			Mean.		
		T.	Cal.	P. ct.	T.	Cal.	P. ct.	T.	Cal.	P. ct.
0-10	8.42	21.3	14,600	49.2	21.1	14,400	46.6	20.6	14,000	47.5
10-20	6.88	16.1	8,300	28.0	16.4	8,500	27.5	17.3	9,100	31.0
20-30	6.27	8.8	3,000	10.1	9.1	3,200	10.4	9.0	3,100	10.5
30-40	5.79	6.9	1,700	5.7	7.1	1,800	5.8	6.4	1,400	4.8
40-50	5.12	5.7	880	3.0	6.3	1,200	3.9	5.5	770	2.6
50-60	4.52	4.9	410	1.4	5.7	750	2.4	4.9	410	1.4
60-70	4.03	4.8	320	1.1	5.1	440	1.4	4.6	260	.9
70-80	3.60	4.5	180	.6	4.7	250	.8	4.5	160	.5
80-100	5.89	4.4	210	.7	4.5	290	.9	4.3	190	.7
100-133	4.09	4.3	120	.4	4.2	80	.3	4.2	90	.3
	54.61	9.44	29,720	....	9.66	30,910	....	9.40	29,480	....

SENECA LAKE.

Depth in meters.	R. T.	1910			1911			1914		
		T.	Cal.	P. ct.	T.	Cal.	P. ct.	T.	Cal.	P. ct.
0-10	9.35	19.6	14,600	44.4	19.6	14,600	49.5	20.3	15,200	40.1
10-20	8.40	15.7	9,600	29.2	16.2	10,200	34.5	19.2	12,800	33.8
20-30	7.86	8.7	3,700	11.2	7.3	2,600	8.8	11.4	5,800	15.3
30-40	7.41	6.4	1,800	5.5	5.8	800	2.7	7.1	2,300	6.1
40-50	6.92	5.5	1,000	3.0	4.6	400	1.3	5.4	970	2.6
50-60	6.49	4.9	600	1.8	4.4	280	1.0	4.7	450	1.2
60-70	5.89	4.8	450	1.4	4.3	160	.6	4.4	240	.6
70-80	5.52	4.6	320	1.0	4.3	160	.6	4.2	110	.3
80-100	9.82	4.5	460	1.4	4.2	200	....	4.0	....	....
100-130	12.14	4.2	200	....	4.1	100	....	4.0	....	....
130-150	5.76	4.2	100	....	4.0	80	....	4.0	....	....
150-188	3.22	4.2	70	....	4.0	....	....	4.0	....	....
	....	7.71	32,900	....	7.34	29,600	....	8.27	37,870	....

Depth in meters.	R. T.	1918			Mean.		
		T.	Cal.	P. ct.	T.	Cal.	P. ct.
0-10	9.35	20.5	15,400	42.7	19.9	14,900	43.8
10-20	8.40	17.2	11,100	30.8	17.1	10,960	32.4
20-30	7.86	9.9	4,600	12.7	9.3	4,200	12.4
30-40	7.41	6.8	2,100	5.8	6.3	1,700	5.0
40-50	6.92	6.0	1,400	3.9	5.4	940	2.8
50-60	6.49	5.2	760	2.1	4.6	420	1.2
60-70	5.89	4.4	230	.6	4.5	270	.8
70-80	5.52	4.3	160	.4	4.3	180	.5
80-100	9.82	4.2	190	.8	4.2	260	.8
100-130	12.14	4.1	120	.3	4.1	130	.4
130-150	5.76	4.0	....	....	4.0	40	.1
150-188	3.22	4.0	....	....	4.0	20	....
	....	8.07	36,060	....	7.84	34,020	....

DISTRIBUTION OF HEAT.

The radiation from the sun which enters a lake is rapidly absorbed by the strata of water near the surface. Even in very clear lakes only 20 per cent of the total radiation passes the 1-meter level, and only about 10 per cent passes the 3-meter level. (See p. 228.) All of the warming of the deeper water and most of the warming of that which lies below the surface meter is due not to insolation but to mixture of warmer water carried down from near the surface. This mixture of warm surface water with the cooler water below is effected by the wind for all temperatures above 4°. It involves work against gravity, since the warmer water is lighter than the cooler. This work may be measured and may be conveniently stated in gram-centimeters per square centimeter of lake area. These facts were stated in our paper on the New York Lakes (Birge and Juday, 1914, p. 562). The principles underlying these ideas were later published as a special paper (Birge, 1916, pp. 341–391) and were applied to Lake Mendota. It was there shown that about 1,210 gram-centimeters of work per square centimeter of area are needed to distribute 18,400 gram-calories of heat per square centimeter of area through the waters of a lake 24 meters in maximum depth and 12.1 meters in mean depth. It is understood that in this statement the term "work" is not used in an exact sense; since in it are included both the action of the wind in distributing heat, which is properly work; and also the direct effect of insolation, which does not involve work. (See Birge and Juday, 1914, p. 574; Birge, 1916, p. 360.) This division of the distribution of heat between sun and wind is discussed later in the paper. For the present, however, the matter is discussed as though the entire distribution of heat were due to wind.

TABLE 4.—TEMPERATURE (T) IN DEGREES CENTIGRADE AND GRAM CENTIMETERS (G. CM.) OF WORK NECESSARY TO DISTRIBUTE THE SUMMER HEAT INCOME.

[NOTE.—This table shows the "direct curve of work," i. e., the work necessary to carry the warmed water from the surface to the stratum in question. It is stated in gram centimeters per square centimeter of surface of the lake.]

CANANDAIGUA LAKE.

Depth in meters.	1910		1911		1914		1916		1918		Mean.	
	T.	G. cm.	T.	G. cm.	T.	G. cm.	T.	G. cm.	T.	G. cm.	T.	G. cm.
0–5	21.6	236.2	20.0	224.0	21.5	240.8	21.5	240.8	21.1	224.0	21.1	224.0
5–10	21.0	582.0	19.6	505.3	20.7	574.1	21.3	613.0	20.6	568.1	20.6	568.1
10–15	18.0	630.7	17.5	589.5	16.9	539.3	17.8	612.4	17.0	548.4	17.5	589.5
15–20	10.6	199.1	10.6	199.1	10.2	176.6	12.0	288.3	12.5	309.6	11.2	235.5
20–25	8.2	100.4	6.2	25.8	7.4	62.7	9.2	149.8	9.8	191.9	8.2	100.4
25–30	7.0	60.8	5.4	13.7	6.9	56.5	8.0	106.1	8.0	106.1	7.1	64.2
30–40	6.2	75.2	4.9	13.9	6.3	83.2	6.6	104.9	6.8	122.8	6.1	69.3
40–50	5.8	57.2	4.6	6.6	5.4	35.2	5.9	63.8	5.9	63.8	5.5	39.6
50–60	5.6	42.0	4.5	4.0	4.8	10.0	5.5	36.0	5.6	42.0	5.2	24.0
60–70	5.5	22.3	4.4	1.2	4.6	3.7	5.3	17.4	5.4	19.8	5.1	12.4
70–84	5.4	6.7	4.5	.4	4.5	.8	5.0	3.3	5.3	5.8	4.9	2.9
	....	2,022.6	....	1,583.5	....	1,782.9	....	2,235.8	....	2,202.3	....	1,929.9

TABLE 4.—TEMPERATURE (T) IN DEGREES CENTIGRADE AND GRAM CENTIMETERS (G. CM.) OF WORK NECESSARY TO DISTRIBUTE THE SUMMER HEAT INCOME—Continued.

CAYUGA LAKE.

Depth in meters.	1910		1911		1914		1917		1918		Mean.	
	T.	G. cm.	T.	G. cm.	T.	G. cm.	T.	G. cm.	T.	G. cm.'	T.	G. cm.
0-5	19.6	187.6	20.0	195.4	21.4	229.8	21.8	239.8	21.4	237.5	20.8	215.3
5-10	19.6	488.4	19.9	497.1	21.4	598.2	20.7	554.9	20.8	560.7	20.5	540.4
10-15	19.4	727.6	19.6	745.3	20.9	864.4	18.8	674.7	19.3	718.8	19.6	745.3
15-20	16.0	603.6	14.9	503.4	16.7	673.9	13.2	363.9	13.4	379.1	14.8	494.6
20-25	9.9	189.6	9.0	137.9	11.0	264.2	9.8	183.8	10.0	196.1	9.9	89.6
25-30	7.8	95.0	6.9	56.0	8.0	105.2	7.7	90.7	8.2	115.3	7.7	90.7
30-40	6.4	94.9	5.6	30.3	6.2	70.7	6.9	133.3	7.1	147.5	6.4	92.9
40-50	5.4	41.6	4.7	5.8	5.2	20.8	5.9	53.1	6.3	97.0	5.5	41.6
50-60	4.9	17.4	4.4	5.0	4.6	6.2	4.9	17.4	5.7	54.8	4.9	17.4
60-70	4.6	9.2	4.4	2.6	4.4	2.6	4.8	13.1	5.1	26.2	4.6	9.2
70-80	4.5	5.4	4.3	2.7	4.3	2.7	4.5	5.4	4.7	12.1	4.5	4.0
80-100	4.5	10.6	4.2	....	4.1	....	4.4	5.3	4.5	10.6	4.3	5.3
100-134	4.4	7.2	4.2	....	4.1	....	4.3	4.8	4.2	....	4.2	....
	....	2,478.1	....	2,181.5	....	2,838.7	....	2,340.2	....	2,555.7	....	2,446.3

SENECA LAKE.

Depth in meters.	1910		1911		1914		1918		Mean.	
	T.	G. cm.	T.	G. cm.	T.	G. cm.	T	G. cm.	T.	G. cm.
0-5	19.8	205.9	19.7	203.5	20.4	220.2	20.6	226.1	20.1	213.0
5-10	19.4	552.8	19.2	539.4	20.2	603.0	20.5	626.4	19.8	579.6
10-15	17.8	718.2	17.8	718.2	20.1	959.4	20.2	975.5	19.2	863.0
15-20	13.3	457.8	14.0	526.3	18.0	996.4	14.0	526.3	14.8	609.4
20-25	9.3	194.6	8.0	112.2	13.4	585.5	11.5	380.1	10.6	296.8
25-30	7.9	126.3	6.3	44.9	9.4	237.5	8.2	145.5	8.0	132.7
30-40	6.4	119.6	5.8	67.6	7.1	195.0	6.8	161.2	6.3	109.2
40-50	5.5	56.0	4.6	9.3	5.4	49.8	6.0	99.5	5.4	49.8
50-60	4.9	24.6	4.4	3.5	4.7	14.0	5.2	42.1	4.6	10.5
60-70	4.8	19.0	4.3	3.8	4.4	3.8	4.4	3.8	4.5	7.6
70-80	4.6	22.0	4.3	5.5	4.2	....	4.3	5.5	4.3	4.5
80-100	4.5	19.6	4.2	....	4.0	....	4.2	....	4.2	....
100-130	4.2	....	4.1	....	4.0	....	4.1	....	4.1	....
130-150	4.2	....	4.0	....	4.0	....	4.0	....	4.0	....
150-188	4.2	....	4.0	....	4.0	....	4.0	....	4.0	....
	....	2,516.4	....	2,234.2	....	3,864.6	....	3,192.0	....	2,876.1

DIRECT WORK.

Table 4 shows the distribution of heat for the lakes under consideration. The results of the computation only are given; the details of the method being quite similar to those illustrated in the paper before referred to (Birge, 1916) and also in Table 5, page 220, of this paper. Taking the means only it appears that in Canandaigua Lake about 1,930 g. cm. of work per square centimeter of the area of the lake are needed to distribute about 27,000 cal. of heat through the water, the depth of which is 84 m. In Cayuga Lake about 2,450 g. cm. of work distribute 29,500 cal. in water, the maximum depth of which is 133 m.; in Seneca Lake 2,880 g. cm. distribute 34,000 cal. in water the maximum depth of which is 188 m.

The amount of work needed to carry the heat to the corresponding stratum of the several lakes varies with the loss of density of the water due to rise of temperature and with the quantity of water in the stratum. The latter factor is represented by the reduced thickness of the stratum. (See Table 3.) The first factor is the more variable in these lakes, and to it are due most of the striking differences in the work required to warm the deeper strata. In the 30 to 40 m. stratum of Canandaigua Lake, for instance, it required about 70 g. cm. to put 1,230 cal. into place. In the corresponding stratum of Cayuga Lake it required 93 g. cm. to place 1,400 cal. The difference in calories is about 14 per cent, in work over 30 per cent. This is mainly due to the difference in loss of density. At 6.1°, the temperature of Canandaigua Lake, this is 35 points,[1] and at 6.4°, the temperature of Cayuga Lake, it is 46 points, or over 30 per cent greater.

Table 4 shows that a great amount of work is necessary to produce by mixture the high temperature of the upper strata; it shows also that an almost incredibly small amount of work is needed to carry considerable heat to great depths if only it involves but little rise of temperature. Note, for example, Seneca Lake, where 42 cal./cm.^{2} of surface are transported to a mean depth of 55 m. for an expenditure of about 1 g. cm. On the other hand, in the corresponding stratum of Canandaigua Lake, each gram centimeter of work transports only about 18 cal. The difference is due to the much greater rise of temperature in the smaller lake—reaching 5.2° instead of 4.5° in Seneca Lake.

TABLE 5.—DETAIL FOR SENECA LAKE OF THE FACTS OF DISTRIBUTION OF MEAN SUMMER HEAT INCOME.

[NOTE.—T.=temperature in degrees centigrade; 1-D=loss of density due to warming; RT×Z=factor, reduced thickness multiplied by depth. Direct=work done *in behalf of* stratum in question; Dist.=work done *in* stratum in question; Cal.=calories of summer heat income in stratum. All expressed in units per square centimeter of lake surface. See fig. 3, p. 229; also Birge, 1916, p. 349, 355.]

Depth in meters.	T.	1-D.	RT×Z.	Direct work.		Dist. work,		Cal.	Depth in meters.	G. cm.	Cal.
				G. cm.	G. cm.	G. cm.	G. cm.				
0-1	20.4	0.001853	49.5	9.2		284.6		1,624	0	2,874.4	34,020
1-2	20.2	1815	147	26.8		266.5		1,588	1	2,589.8	32,396
2-3	20.2	1815	240	43.7		248.8		1,555	2	2,323.3	30,808
3-4	20.1	1790	333	59.6		231.5		1,530	3	2,074.5	29,253
4-5	20.0	1770	423	74.9	214.2	213.6	1,245.0	1,504	4	1,843.0	27,723
5-6	20.0	1770	512	90.6		197.0		1,488	5	1,629.4	26,219
6-7	19.9	1749	592	103.6		180.8		1,447	6	1,432.4	24,731
7-8	19.8	1729	675	117.8		164.9		1,422	7	1,251.6	23,284
8-9	19.7	1708	748	127.9		149.6		1,382	8	1,086.7	21,862
9-10	19.7	1708	827	141.4	581.3	134.6	826.9	1,366	9	937.1	20,480
10-11	19.6	1688	914	154.5		119.8		1,357	10	802.5	19,114
11-12	19.5	1668	989	165.2		105.2		1,333	11	682.7	17,757
12-13	19.3	1628	1,076	176.0		90.9		1,316	12	577.5	16,424
13-14	18.8	1519	1,147	176.0		76.5		1,258	13	486.6	15,108
14-15	18.6	1491	1,232	183.3	855.0	65.6	457.0	1,241	14	410.1	13,850
15-16	17.4	1269	1,304	165.7		53.0		1,126	15	345.5	12,609
16-17	16.0	1030	1,370	141.1		43.3		996	16	292.5	11,483
17-18	14.8	0844	1,453	123.4		35.6		896	17	249.2	10,487
18-19	13.6	0674	1,517	102.4		29.3		787	18	213.6	9,591
19-20	12.0	0475	1,580	74.6	607.2	24.6	185.8	648	19	184.3	8,804
20-25	10.6	0328	9,050		296.8		80.8	2,653	20	159.7	8,156
25-30	8.0	0124	10,735		132.7		35.7	1,560	25	78.9	5,503
30-40	6.3	0042	26,040		109.2		29.5	1,714	30	43.2	3,943
40-50	5.4	0016	31,130		49.8		9.1	969	40	13.7	2,229
50-60	4.6	0003	35,120		10.5		2.9	485	50	4.6	1,260
60-70	4.5	0002	38,005		7.6		1.3	263	60	1.7	775
70-80	4.3	0001	45,280		4.5		.4	165	70	.4	512
Below 80								347	80	.0	347
Total					2,868.8		2,874.4	34.020			

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[1] By a "point" is meant a decrease in density of one part per million. The density of water at 6.1 as compared with that at 4.0° is 0.999965. The loss in density is, therefore, 0.000035 and this represents the loss in weight of the lighter surface water at 6.1°, and, therefore, is one factor in determining the work to be done in pushing it down into deeper and cooler strata. For convenience in computation this factor is taken as a positive quantity and a whole number is stated as 35 points. (See Birge, 1916, p. 391.)

DISTRIBUTED WORK.

Table 4 deals with the *direct curve of work*. It gives for each stratum the amount of work necessary to convey the warmer and lighter water from the surface to the depth in question, assuming that the lower water has a temperature of 4.0°. In warming all strata below that at the surface most of the work is performed in the strata above that for the benefit of which the work is done. If the work for each stratum is thus distributed to the several strata above it, we derive the *curve of distributed work*. (See Birge, 1916, p. 355). This is shown for the mean of each lake in Table 6 and for Seneca Lake in figure 3. The numbers for each stratum show how many gram centimeters are necessary to distribute through the stratum the heat retained in it and to convey through it the heat which goes on to lower strata. The table shows how shallow is the stratum which receives most of the work of the wind. More than 94 per cent of this work is expended in conveying the heat through the upper 20 m. of the lake. While the effect of the wind extends to the bottom, even in Seneca Lake, the work done in the deeper water is very small, as measured by the fall in density due to increased temperature. In the upper 5 m. are found from 43 to 50 per cent of the work and in this stratum the largest deductions from the apparent work are to be made for the influence of direct insolation.

TABLE 6.—DISTRIBUTED WORK, MEAN.

[NOTE.—This shows work done in each stratum in distributing the heat brought to it, and in carrying on to the next stratum the heat which passes through it. This is computed only for the means of the lakes.]

Depth in meters.	Canandaigua Lake.		Cayuga Lake.		Seneca Lake.	
	G. cm.	Per cent.	G. cm.	Per cent.	G. cm.	Per cent.
0–5	965.4	50.0	1,100.5	45.0	1,245.0	43.4
5–10	548.5	28.4	698.1	28.5	826.9	28.8
10–15	239.3	12.4	367.3	15.1	457.0	15.9
15–20	83.8	4.3	136.6	5.6	185.8	6.5
20–30	58.4	3.1	97.1	4.0	116.5	4.1
30–40	20.0	.9	28.3	1.2	29.5	1.0
40–50	9.1	.4	10.4	.4	9.1	.3
50–60	3.6	.2	4.2	.2	2.9	.1
60–70	1.0	.1	1.8	.1	1.3	....
70–80	.1	....	.9	....	.4	....
80–100	....	....	.3	....	....	....
	1,929.2	....	2,445.5	....	2,874.4	....

SUBTRACTION CURVES.

Table 7 shows the data for the mean subtraction curves of the three lakes. (See Birge, 1916, p. 384.) It shows the number of calories which pass through the several levels of the lakes and the amount of work needed to distribute them through the water below these levels. Comparison of the data at the surface shows that 12 to 14 cal. of heat are distributed through the subjacent water by 1 g. cm. of work. At lower levels the temperature declines and the decrease in density falls off even more rapidly with the result that an increasingly large number of calories is distributed by 1 g. cm. of work. At the depth of 10 m. the ratio is 25 to 30 cal. to 1 g. cm.; at 20 m. the ratio rises to 40:1 or 50:1; at 30 m. in Seneca Lake and at 40 m. in the others it has risen nearly or quite to 100:1. This relation explains how in lakes of great depth a large quantity of heat is carried in spring to the lower water. The great quantity of work needed for distribution in the upper water as the temperature rises equally makes clear the reason why the lower water soon ceases to gain heat as the season advances.

In Seneca Lake work amounting to only 0.4 g. cm. is needed to distribute 512 cal. to depths below 70 m., while no appreciable amount of work is needed to distribute 347 cal. through the water below 80 m. The last statement is obviously not strictly accurate, but it is not worth while to compute the work in those cases where the decrease in density due to increase of temperature is less than one part per million.

TABLE 7.—SUBTRACTION CURVE MEANS: AMOUNT AND PER CENT OF HEAT IN SUMMER HEAT INCOME AND OF WORK NECESSARY TO DISTRIBUTE THIS HEAT FOUND AT THE SURFACE AND AT DIFFERENT DEPTHS OF THE SEVERAL LAKES.

[NOTE.—Stated in units per square centimeter of the surface of the lakes.]

Depth in meters.	Canandaigua Lake.				Cayuga Lake.				Seneca Lake.			
	Cal.	P. ct.	G. cm.	P. ct.	Cal.	P. ct.	G. cm.	P. ct.	Cal.	P. ct.	G. cm.	P. ct.
0	26,980	100.0	1,929	100.0	29,480	100.0	2,446	100.0	34,020	100.0	2,874	100.0
5	19,140	70.9	964	50.0	21,860	74.1	1,345	55.0	26,220	77.2	1,629	56.8
10	12,460	46.2	415	21.6	15,480	52.5	647	26.5	19,120	56.3	802	28.0
15	1,500	27.8	176	9.2	9,980	33.8	280	11.4	12,610	37.1	345	12.0
20	4,980	18.4	92	4.9	6,380	21.6	143	5.8	8,160	24.0	159	5.6
30	2,640	9.8	34	1.8	3,280	11.1	46	1.8	3,960	11.7	43	1.5
40	1,410	5.2	14	.8	1,880	6.4	18	.6	2,260	6.7	13	.5
50	670	2.5	5	.2	1,110	3.8	8	.2	1,320	3.9	4	.2
60	280	.9	1	.1	700	2.4	4	.0	900	2.6	1	.0
70	40	.15	0	.0	440	1.5	2		630	1.8		
80	0				280	1.0	0		450	1.3		
100					90	.5			190	.6		
130					0				60	.2		
150									20	.0		
188									0			

HEAT AND WORK AS MEASURED AT DEPTH.

In Table 7 the data are given in terms of the surface of the lake—so many calories, or gram centimeters, per square centimeter of surface. If the datum plane is taken as the area of the lake at the depth in question, the number of calories and gram centimeters at each level will be increased proportionally to the decrease of area as compared with that of the surface; but the ratio between the amounts of work and of heat would remain unaltered. This relation is shown in Table 8. Perhaps the most interesting fact shown by it is the very close agreement between Cayuga and Seneca Lakes in both heat and work after the surface level is passed. Approximately equal quantities of heat pass through the 5 to 40 m. levels of both lakes. Cayuga Lake shows at the surface considerably less heat per unit of area than Seneca has, but this is largely due to the great area of shallow water at the north end of Cayuga Lake. No such area is found anywhere in Seneca Lake. The area of Cayuga Lake at 5 m. is about 79 per cent of the surface area, while that of Seneca Lake at the same depth is 87 per cent of the surface. The area of the 10 m. level in Cayuga is about 92 per cent of that at 5 m., and in Seneca about 93 per cent of the 5 m. level, a very close correspondence, which shows itself in the heat and work. The large area of shallow water in Cayuga Lake adds nothing to its effective area in absorbing heat, nor does it seem to diminish the efficiency of the lake. Canandaigua Lake, however, is plainly less efficient than either of the others. Its smaller area and higher banks cause this condition, since both factors lessen the efficiency of the wind. (See Birge and Juday, 1914, Pls. CXIII, CXIV, CXVI.)

TABLE 8.—AMOUNT OF HEAT IN SUMMER HEAT INCOME AND WORK NECESSARY TO DISTRIBUTE IT.

[NOTE.—Expressed in units per square centimeter of the depth in question; not (as in other tables) in units per square centimeter of the lake surface.]

Depth in meters.	Canandaigua Lake.		Cayuga Lake.		Seneca Lake.	
	Cal.	G. cm.	Cal.	G. cm.	Cal.	G. cm.
0	26,980	1,929	29,480	2,446	34,020	2,874
5	22,970	1,150	27,750	1,710	28,000	1,740
10	16,540	549	21,440	892	21,900	922
15	10,560	246	14,530	406	14,900	410
20	7,350	136	9,800	220	10,100	197
30	4,340	56	5,420	76	5,190	56
40	2,630	26	3,440	33	3,150	17
50	1,520	11	2,330	17	1,980	6
60	830	4	1,640	9	1,480	1.7
70	40		1,150	5	1,110	
80			820		840	
100			300		420	
130					170	
150					90	
188					0	

ABSORPTION OF SUN'S ENERGY.

Observations were made in 1918 on Seneca, Cayuga, and Canandaigua Lakes in order to ascertain the rate at which the energy of the sun's rays is absorbed by the water of the lakes. The instrument is described in another paper (Birge, 1921), and the description will not be repeated. It consists of a receiver containing 20 small thermal couples which can be lowered into the lake to any desired depth and alternately exposed to the sun and covered. The electrical effect of the sun's radiation on the thermal couples is proportional to the energy in its rays, and the resulting electrical currents are measured by the deflections caused in a d'Arsonval galvanometer. The galvanometer is kept on shore and is connected with the receiver by an insulated cable 100 m. long.

The observations on the three lakes afford excellent illustrations of the results obtainable by this instrument, and also of the difficulties which necessarily attend observations of the kind if made in the course of a short visit, when every opportunity must be fully used. The general results from each lake are clear and unmistakable, but in each case the details are affected by special conditions of sky or water.

A part of the observations on Seneca Lake is given in Table 9 in order to show the nature of the data.

TABLE 9.—TRANSMISSION OF SUN'S ENERGY BY THE WATER OF SENECA LAKE OFF HECTOR POINT, N. Y., AUG. 1, 1918.

[NOTE.—1.50 to 2.23 p. m., Government time=12.40 to 1.11 sun time. Transparency 6.8 m.]

Hour, p. m.	Depth in centimeters.	Zero.	Reading.	Deflection.
1.50	0	10.5 10.0	127.8 126.7	117.0
1.55	25	13.5 13.0	83.0 84.0	70.3
1.57	50	13.0 13.0	77.0 77.0	64.0
1.58	100	12.5 12.5	59.5 50.0	47.3
1.59	150	12.5 12.5	50.5 51.5	38.5
2.00	200	12.5 12.2	45.8 45.5	33.2
2.01	250	12.2 12.0	40.6 40.2	28.3
2.03	300	12.1 12.0	35.8 36.5	24.1
2.05	350	12.3 12.1	32.3 32.1	20.0
2.07	400	12.1 12.1	29.2 29.2	17.1
2.09	500	12.2 12.2	24.2 24.0	11.9
2.12	600	12.1 12.1	20.3 20.5	8.3
2.14	700	12.2 12.2	18.1 18.1	5.9
2.17	800	12.2 12.2	16.2 16.1	4.0
2.18	900	12.1 12.3 12.2	15.1 15.1 15.0	2.9
2.23	1,000	12.2 12.2 12.2 12.4 12.3	14.5 14.4 14.6 14.6	2.2

NOTES ON ABOVE TABLE.

1. Sky perfectly clear and sun's radiation steady; no clouds; practically no haze. Light south air, causing ripples on surface. Some swell from wind of yesterday and of early morning. The swell caused irregularities of reading in upper water, as it raised and lowered the boat. At 100 cm. the scale moved over 4 to 5 divisions, and reading had to be estimated under these conditions. This effect became less as depth increased. Ripples cause a quivering of the reading in the galvanometer but are too small to cause swings of the scale.

2. In reading the direct sun a shunt coil is included in the circuit in order to keep the reading within the limits of the scale. This coil is cut out by a switch when the receiver is used in water. The reading in air must be multiplied by 1.89 to reduce it to the same scale as those in the water. Its value, therefore, on this occasion is 221 divisions. One division equals 0.059 cal./cm.^{2}/min., so that the sun was delivering about 1.30 cal./cm.^{2}/min.

3. The observations not reported included a repetition of several of the readings, and a second reading in the air, which gave a value of 116.2 divisions, or substantially the same as the first reading.

4. The numbers in the columns headed *zero*, *reading*, *deflection*, indicate divisions of the scale of the galvanometer.

From these readings may be computed the value of the energy delivered by the sun at different depths of the lake, as is shown in the following table:

TABLE 10.—CALORIES PER SQUARE CENTIMETER PER MINUTE FOUND AT VARIOUS DEPTHS OF SENECA LAKE, AUG. 1, 1918.

Depth in centimeters.	Per cent.	Cal./cm.^{2}/min.	Depth in centimeters.	Per cent.	Cal./cm.^{2}/min.	Depth in centimeters.	Per cent.	Cal./cm.^{2}/min.
In air	100.0	1.30	250	12.8	0.17	700	2.7	0.035
25	31.8	.41	300	10.9	.14	800	1.8	.023
50	29.0	.38	350	9.0	.12	900	1.3	.017
100	21.4	.28	400	7.7	.10	1,000	1.0	.013
150	17.4	.23	500	5.4	.07			
200	15.0	.20	600	3.8	.05			

TABLE 11.—TRANSMISSION OF SUN'S ENERGY PER METER OF DEPTH.

[NOTE.—Per cent of the energy found at the upper surface of each 1 m. stratum which is present at the lower surface of such stratum.]

Stratum in meters.	Transmission, per cent.	Stratum in meters.	Transmission, per cent.	Stratum in meters.	Transmission, per cent.
0–1	21.4	4–5	69.6	8–9	72.2
1–2	70.2	5–6	69.8	9–10	75.9
2–3	72.6	6–7	71.1		
3–4	71.0	7–8	67.8		

Table 11 is given as it stands in order to bring out the various small variations in percentage which are inherent in the observations. In all cases the fraction of a division of the galvanometer scale must be estimated and is, therefore, subject to error. The value taken as zero is not a fixed one and in any observation may be recorded slightly too low, or more probably a little too high. The motion of the boat, due to the swell, as stated above, might introduce some errors in this case, especially in the readings from the upper water. In figure 2 the results are plotted and a smooth curve *a–a* is drawn through them. All of the observations are very close to the curve. It is plain that there was transmitted through each 1 m. stratum of water below the surface meter about 71 per cent of the energy received at its upper surface. It is not probable that the higher transmission indicated in the 9 to 10 m. stratum has any significance. A reading of 2.1 divisions of the scale at 10 m. instead of 2.2 divisions would bring this interval into line with the others.

Lake water differs widely from pure water in the quantity of energy transmitted. If we assume a solar energy curve corresponding to a path of the rays in the air of 1.5 atmosphere, with about 0.5 cm. condensable water in the atmosphere, about 47 per cent of the solar energy will be left after passing through 1 m. of pure water. The water of Seneca Lake, therefore, cuts off about 25 per cent more than does pure water and adds one-half to the loss due to pure water. Pure water transmits through the 1 to 2 m. stratum nearly 80 per cent of the energy reaching its upper level and over 90 per cent passes through all deeper 1 m. strata, the loss per meter rapidly declining to a minimum of about 2 per cent of the energy incident on the upper surface of the stratum. At 5 m., therefore, there would remain about 29 per cent of the original energy of the sun and about 23.4 per cent at 10 m. instead of 5.4 per cent and 1 per cent found in Seneca Lake. This wide difference between pure water and the lake water is probably due chiefly to matter suspended in the water of Seneca Lake, since there is very little stain present in the water. The suspended matter is partly organic but chiefly fine silt derived from the soft shales that constitute much of the shores.

In pure water the transmission through the 1 to 2 m. stratum is much smaller than in those below. This is due to the rapid absorption of the rays of the red end of the spectrum as compared with the slow absorption of the shorter waves. No such effect seems to be present in the lake, nor is it ordinarily demonstrable in lakes. Sometimes, but not commonly, the deeper strata of a lake show a transmission 1 or 2 per cent higher than the 1 to 2 m. stratum, but in general the transmission in that stratum is nearly the same as in those immediately below. This means that the large nonselective absorption due to turbidity and the selective absorption due to stain obscure the selective absorption of the water, as water, after the first meter has been passed. In that meter of water is absorbed practically all of the energy contained in that part of the spectrum lying below the *A* line which is commonly taken as the lower limit of the visible spectrum.

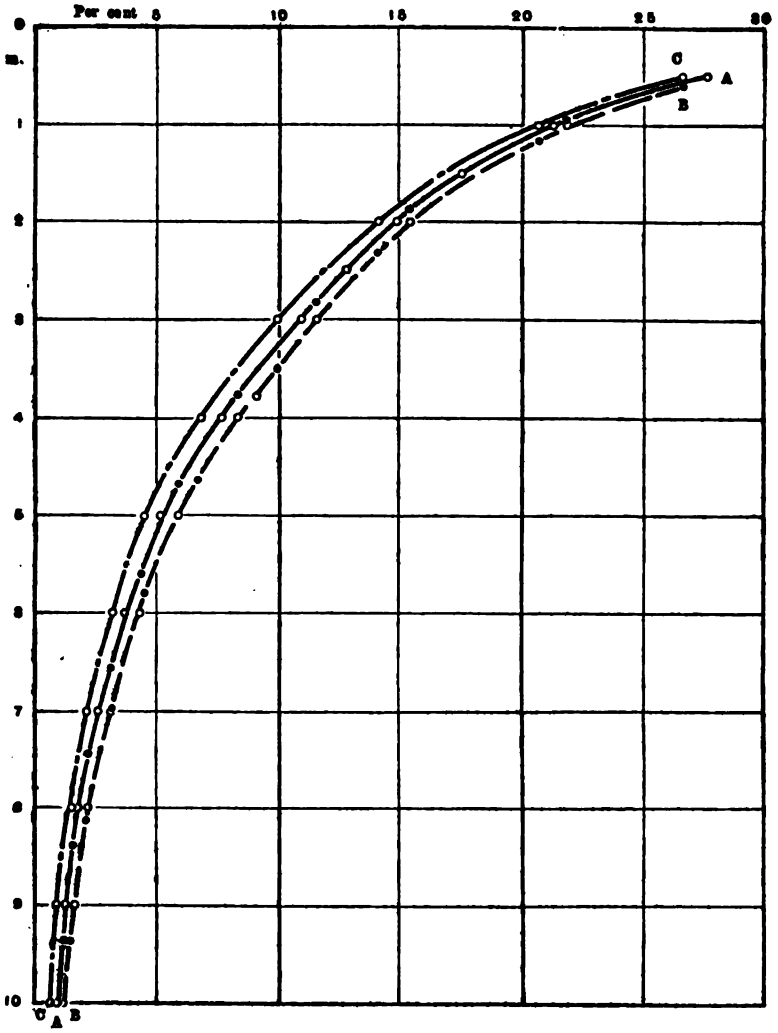

FIG. 2.—Curves of transmission of sun's radiation, Seneca Lake, Aug. 1, 1918. The vertical axis gives depth and the horizontal axis gives per cent of the total radiation of the sun. *A–A*, direct observations; *B–B*, vertical sun; *C–C*, mean sun. The sun's rays passed through a thickness of 100 cm. water of the lake at the depth of 94 cm. Dots are placed corresponding to this depth on the curve *A–A*, and from these is plotted the curve *B–B*, for the sun in the zenith when depth and stratum traversed by rays are equal. The rays pass through a mean distance of 115 cm. during the warming season in reaching a depth of 100 cm. These points are marked on the curve *B–B*, and from them is plotted the curve *C–C* or the curve of mean sun. (See Table 12, p. 228.)

The general result of these observations is, therefore, plain. Under the conditions of the time and place 21 to 22 per cent of the sun's energy delivered to the surface was present at a depth of 1 m. In the deeper 1 m. strata there was a loss of 28 to 29 per cent of the energy present at the upper surface of the stratum. At 5 m. depth there remained about 5.4 per cent, and at 10 m. about 1 per cent of the energy delivered to the surface.

We may infer from such a set of observations the penetration of the sun's rays during the whole day or during a longer period, assuming that the turbidity and color of the water remain unchanged. In such a process it is not hard to secure results which are correct in general, but it is impossible to secure minute accuracy. Certain, though not all, of the facts which prevent minute accuracy will be mentioned.

1. Sunlight is a mixture of the direct rays of the sun and of rays reflected from the sky. The percentage of sky radiation is very variable, being sometimes as low as 8 per cent of the total radiation and rising nearly to 100 per cent when the sun barely shines through haze or cloud. The quantity of energy reflected from a unit area of sky is also variable and differs with the nature of the sky and the proximity of the area to the sun. The mean percentage of sky radiation reflected from the surface of the water differs from that of the direct rays, and the mean path in water of the rays from the sky differs from that of the direct rays. It is practically impossible, under the conditions of observations on lakes, to determine either the amount or the distribution of the sky radiation. It is, therefore, impossible to make full correction for the elements in the mixture of direct and diffuse rays at the time of observations.

2. It is also impossible to make such corrections for longer periods, since the average amount of sky radiation is still quite unknown for most places, and is not accurately known anywhere.

3. No correction has been made in the observations for radiation reflected from the surface of the water, but the readings at 1 m., etc., have been compared directly with the reading in air. The direct sun radiation, at the altitude of the sun when the observations were made, would lose about 2.1 per cent by reflection. The sky radiation would lose 17.3 per cent if equal quantities came from equal areas of sky. This loss at the surface, which can not be known accurately, has been balanced against the opposite effect of the hemispherical glass cover of the sunshine receiver. There would be about 4 per cent of the sun's radiation reflected from this in air and about 0.5 per cent in water.

In computing a standard curve of absorption for Seneca Lake, all radiation has been referred directly to the sun, and the path of the rays in the water has been computed on that basis, from the following elements:

Time of observations, August 1, 1918, 12.40 to 1.11 sun time.

Corresponding altitude of sun, August 1, 64.1 to 62.3°.

Depth at which sun's rays pass through 1 m. of water, at first observation, 94.5 cm; at last observation, 93.7 cm.; mean 94.1 cm.

On the *curve of direct observations* (*A–A*, fig. 2) are noted the readings at the distances corresponding to this path of the rays in water. These periods are plotted and connected by a new curve, *B–B*, the *curve for vertical sun*. In this curve, which assumes a sun in the zenith, the depth below the surface equals the length of path of the rays in reaching that depth. This constitutes a standard curve, from which may be derived the energy which remains at given depths below the surface at any time of the day or year, provided the altitude of the sun is known and the corresponding length of the path of its rays in water. It must be assumed also that all radiation comes directly from the sun, or at least that the value of the sky radiation is the same as at the time of observation.

The results are stated in Table 12, vertical sun.

The mean distribution of sunshine and cloud at Seneca Lake is not known, but at Madison, Wis., the mean daily supply from sun and sky during the five months April 1 to August 31 is 398 cal. The mean path of the rays during this period to reach a depth of 100 cm. below the surface is 115 cm. In this computation allowance is made for reflection from the surface in excess of 2.1 per cent; all radiation is supposed to come from the sun; and the form—though not the area—of the solar energy curve is supposed to be constant.

The points corresponding to this distance of 115 cm. per 100 cm. of depth are noted on the curve for vertical sun, carried up to their proper place, and a third curve, *C–C*, figure 2, is drawn, which is the curve for mean sun (Table 12).

TABLE 12.—TRANSMISSION OF SUN'S RAYS BY WATER OF SENECA LAKE, AUG. 1, 1918. (See fig. 2, p. 226.)

Depth in centimeters.	Per cent radiation remaining at depth indicated.			Depth in centimeters.	Per cent radiation remaining at depth indicated.		
	Observed per cent.	Computed per cent.			Observed per cent.	Computed per cent.	
		Vertical sun.	Mean sun.			Vertical sun.	Mean sun.
100	21.4	21.9	20.7	600	3.8	4.4	3.3
200	15.0	15.6	14.3	700	2.7	3.2	2.3
300	10.9	11.5	9.9	800	1.8	2.3	1.6
400	7.7	8.3	6.8	900	1.3	1.7	1.0
500	5.4	6.0	4.7	1,000	1.0	1.2	.7

This curve of mean sun and Table 12 show that in Seneca Lake at 1 m. depth there is found an average of about 20.7 per cent of the incident radiation and that each 1 m. stratum below transmits less than 70 per cent of the radiation received by its upper surface. The water has absorbed 99 per cent of the incident energy at about 9 m. as compared with about 10 m. for the observed curve and 11 m. or more for the curve of vertical sun.

The difference in the three curves are not striking in this case; but if the observations had been made at an hour farther from noon, or later in the season, the difference would have been correspondingly larger.

It must not be supposed that this mean sun curve represents exactly the mean conditions actually present during the period when the lake is warming. The transparency of the water is variable and the sun's penetration varies with it. No account is taken in this curve of the energy received during cloudy hours. Yet after all deductions are made it remains true that the curve gives a generally correct picture of the actual direct delivery of the sun's radiation to Seneca Lake so far as a single observation can give this. Hardly more than 20 per cent of the incident energy is delivered to water below the surface meter. Not over 5 per cent is delivered to a greater depth than 5 m. and not over 1 per cent below 10 m. Even a considerable increase in transparency would leave these figures, not unchanged, but of the same order of magnitude.

Observations such as these are ordinarily made at times when the sky radiation is relatively small—near noon of clear days. When, therefore, such an observation is used as the basis of larger conclusions and when in computing the results all radiation is assumed to be direct, the effect of the direct rays of the sun in warming the lake is placed at a maximum. In the preceding paragraph all radiation is supposed to come directly from the sun. In fact at Madison about 16 per cent of the total radiation received April 1 to August 31 comes during cloudy hours, and about 16 per cent more comes from the sky during sunny hours. The direct sun, therefore, supplies only about two-thirds of the radiant energy received by the lake. It may be assumed that during cloudy hours equal areas of sky supply equal amounts of energy to a surface normal to the rays. On this basis, and allowing for reflection from water surface, the mean path of

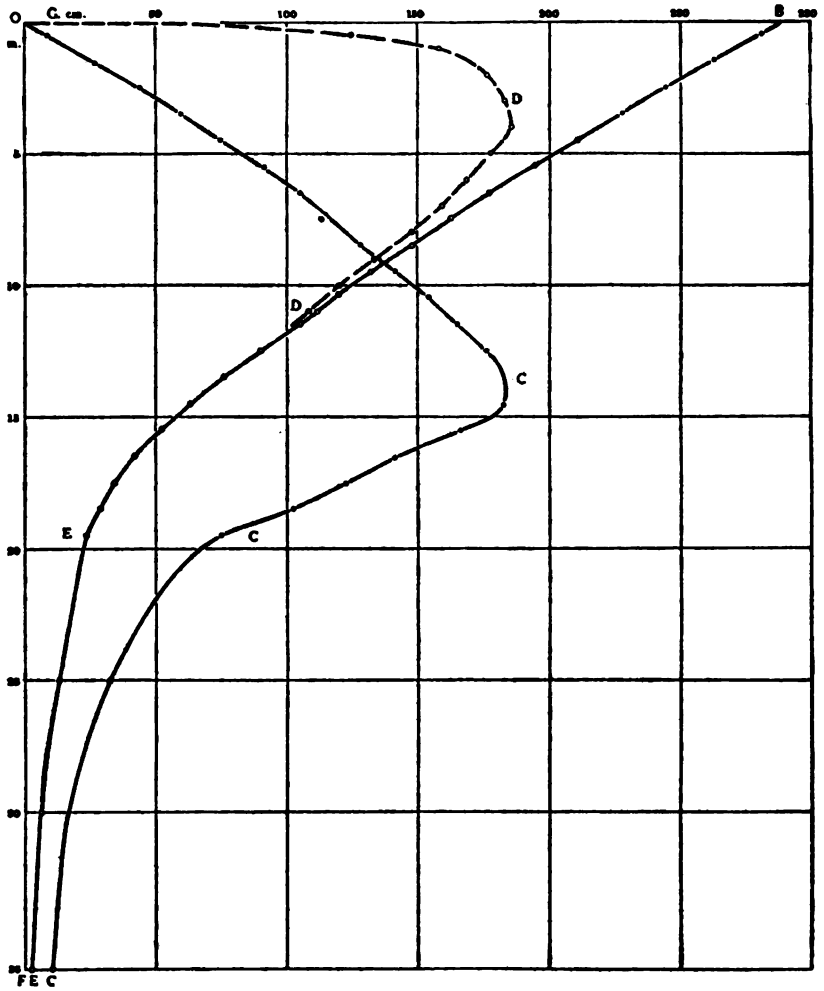

FIG. 3.—Work curves of Seneca Lake, mean temperature. The vertical axis shows depth; the horizontal axis shows gram centimeters of work per meter of depth and square centimeters of surface of lake. *OCC*, curve of direct work. About 145 g. cm. of work, for instance, are necessary to carry the heat of the 9 to 10 m. stratum from the surface and put it in place. *BDE*, curve of distributed work, derived from *OCC*, showing the amount of work done in each 1 m. stratum. The area *OBEFO* (distributed work) is equal to the area *OCCFO* (direct work). *ODD* shows the contribution of the sun in distributing the sun's energy. The area *ODDBO* gives the contribution of the sun, and that of the wind is represented by the area *ODEFO*. (See Table 16, p. 235.)

the diffuse radiation in reaching a depth of 100 cm. would be about 126 cm. as compared with 115 cm. for the direct rays. The mean path for sky radiation during sunny hours would be between the numbers given above, depending on the relative amount of the sky radiation coming from areas close to the sun and, therefore, having approximately the same length of path in the water as the sun's rays have.

In the absence of knowledge of the amount of sky radiation at Seneca Lake, either general or on the date of observation, no correction can be made for sky radiation. Such correction can be made where observations are so numerous that it may safely be assumed that sky radiation was the mean amount. This is the case with Lake Mendota, and the best computation that can be made shows that the mean path of all rays to reach a depth of 100 cm. in the period of April 15 to August 15 is about 118 cm. No essential difference, therefore, is made in the results if all radiation is attributed to the sun with a mean path of 115 cm., as has been done in the previous paragraphs.

The observations on Canandaigua and Cayuga Lakes may be treated much more briefly. They were taken at the same intervals as on Seneca Lake but to the depth of 5 m., which is ample for the determination of the rate of absorption. The results are shown in figures 4 and 5, and summarized in Tables 13 and 14.

TABLE 13.—TRANSMISSION OF RADIATION BY WATER OF CAYUGA LAKE, SHELDRAKE POINT, JULY 29, 1918, 1.45 TO 2.45 P. M., GOVERNMENT TIME. (See fig. 4.)

[NOTE.—Sky with cumulus clouds drifting across; clear between clouds. Transparency of water 6.2 m. Transmission per meter about 66 per cent.]

Depth in centimeters.	Per cent radiation remaining at depth indicated.				Depth in centimeters.	Per cent radiation remaining at depth indicated.			
	Observed per cent.	Mean observed per cent.	Computed per cent.			Observed per cent.	Mean observed per cent.	Computed per cent.	
			Vertical sun.	Mean sun.				Vertical sun.	Mean sun.
100	19.2 19.6	19.4	19.9	17.9	400	5.6 5.4	5.5	6.1	4.9
200	13.4 11.3 11.4	12.8	13.3	11.9	500	3.6 3.4 3.6 3.5 3.7	3.6	4.1	3.1
300	8.1 8.6	8.4	9.1	7.6					

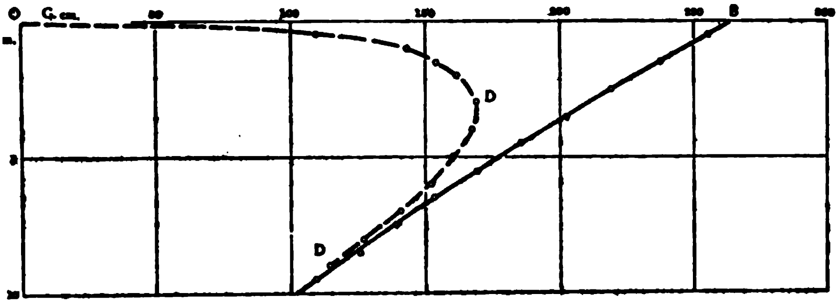

FIG. 4.—Work curves for Cayuga Lake. (See explanation, fig. 3.)

The observations on Cayuga Lake are rendered somewhat irregular by the fact that numerous white cumulus clouds were passing over the sky and work had to be done when the sun was in the spaces between the clouds. Under these conditions the radiation from the sun is sure to be variable; the approach to the sun of a white cloud momentarily raises the radiation and unnoticed wisps of cloud may reduce it. In the series it is clear that the mean of the readings at 200 cm. is too low as compared with all of the others, since the transmission in the 1 to 2 m. stratum should be about the same as below. The value of 12.8 per cent has been assumed, therefore, for the 200 cm. level and a mean transmission of about 66 per cent per meter. Under these conditions about 99 per cent of the sun's energy would be delivered to the upper 8 m. of water, somewhat more than 80 per cent going to the first meter, or with mean sun about 82 per cent.

It will be noted that corresponding with the smaller transparency of the water, as compared with Seneca Lake, the transmission of radiation is decidedly lower.

TABLE 14.—TRANSMISSION OF SUN'S ENERGY BY WATER OF CANANDAIGUA LAKE, JULY 27, 1918, 11.37 A. M. TO 12.03 P. M., GOVERNMENT TIME. (See fig. 5.)

[NOTE.—Sky hazy. Transparency of water 4.4 m. Transmission per meter about 60 per cent.]

Depth in centimeters.	Per cent radiation remaining at depth indicated.			Depth in centimeters.	Per cent radiation remaining at depth indicated.		
	Observed per cent.	Computed per cent.			Observed per cent.	Computed per cent.	
		Vertical sun.	Mean sun.			Vertical sun.	Mean sun.
100	18.7	19.4	18.0	400	4.2	4.8	3.7
200	11.3	12.2	10.7	500	3.1	3.1	2.2
300	6.9	7.8	6.3				

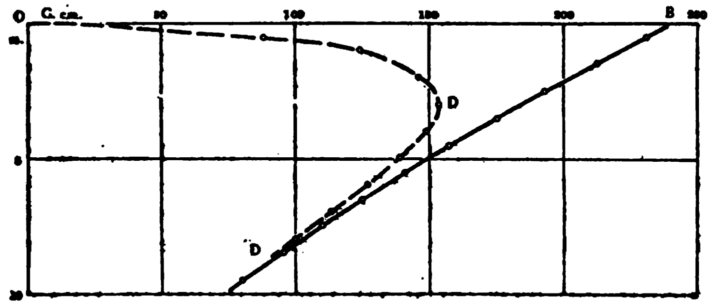

FIG. 5.—Work curves for Canandaigua Lake. (See explanation, fig. 3.)

The observations on Canandaigua Lake were also somewhat irregular, not on account of clouds, but haze. The sky was cloudless, but the hills a few miles up the lake were nearly invisible in the haze which filled the valley. Under such conditions the value of the sun's radiation is much reduced, and it was found to be about 0.95 cal./cm.^{2}/min. as compared with 1.30 cal. in the case of the two other lakes. The readings of the sun at the beginning and end of the observations in the lake were in close agreement. The readings of the first series taken in the water—those taken while the receiver was going down—were also in close agreement and indicate that 18 to 19 per cent of the radiation in air was present at 100 cm. depth and that each meter below that depth transmitted about 60 per cent of the radiation received by its upper surface. At 500 cm., however, the reading rose so that the transmission seemed to rise to about 74 per cent. The second set of readings—those taken while the receiver was being raised—again indicated about 60 per cent transmission but showed at all depths a higher percentage of the radiation at the surface, amounting at 100 cm. to 21 per cent. Comparison with the other lakes shows that the lower value at 100 cm. is to be chosen, as the transparency of the water is decidedly less than in either Cayuga or Seneca Lakes. The haze must have become slightly thinner during the later readings in the water but thickened again before the second reading in the air. The accuracy of the value at 100 cm. must remain somewhat uncertain under the conditions of sky then prevailing. Since the value of the radiation may alter during haze almost from minute to minute with no visible indication of change, such as cloud offers, it would need a very large number of readings to show whether 18 to 19 per cent or a slightly lower figure should be taken as the value for mean sun at 100 cm. The error is not likely to exceed 1 per cent in any case, nor is it large enough to affect general relations of sun to the distribution of heat.

Under these conditions 99 per cent of the sun's energy would be delivered to the upper 6.5 m. of water.

We may now put together the general results from the three lakes in which observations were made.

TABLE 15.—TRANSPARENCY AND TRANSMISSION OF RADIATION—VERTICAL SUN.

	Transparency in meters.	Per cent at 100 centimeters.	Per cent transmission per meter.
Seneca Lake	6.8	21.9	72
Cayuga Lake	6.2	19.9	66
Canandaigua Lake	4.4	19.4	60

In these cases there is some parallelism between the percentage of transmission and the transparency of the lake. This is due to the fact that all these lakes have water which is only slightly stained and which does not differ greatly in color. In general there may be little correlation between transparency and rate of transmission.

WORK OF THE SUN IN DISTRIBUTING HEAT.

From the data at hand it is possible to make a general estimate of the part which the sun plays in distributing the heat gained by Seneca Lake as its summer heat income. We have as data (*a*) the amount of heat so gained as the mean of four seasons; (*b*) the amount and the distribution of the work necessary to carry this heat through the lake, assuming that all work is done by the wind; (*c*) the actual amount of heat delivered into the water of the lake directly by the sun on one date, and the conclusions drawn from these observations in the preceding paragraphs. We lack as data (*a*) the total amount of heat delivered to the lake during the period when the summer heat income is gained; (*b*) the losses of heat during this period from different strata near the surface.

The absence of the data specified and others as well make it impossible to state the rôle of the sun with any approach to exactness. But it is possible to make estimates which will show the general situation and in our almost complete ignorance of the subject, such statements are not without value.

We take, therefore, as the summer heat income of Seneca Lake 34,000 cal./cm.^{2} of surface. Of this sum, 32,400 cal. are found below 1 m.; 28,000 cal. below 5 m.; and 21,900 cal. below 10 m. These figures are based on the calories found per square centimeter of the depth in question, and not those per square centimeter of the surface. In computing the relative work of sun and wind these figures must be used, since the sun's radiation which passes through the shallow water is absorbed by the bottom of the lake.

The distribution of this heat, attributing all work to the wind, requires about 2,874 g. cm. of work per square centimeter of the lake's surface. This work is distributed (fig. 3) at the rate of about 290 g. cm./cm.^{2} of the surface at the surface; 270 g. cm./cm.^{2} at 1 m. depth; 202 g. cm./cm.^{2} at 5 m.; and 125 g. cm./cm.^{2} at 10 m. In the upper 5 m. there is done about 45 per cent of the total work; about 33 per cent in the 5 to 10 m. stratum, both of which are within reach of the direct influence of the sun; about 20 per cent more of the work comes in the 10 to 15 m. stratum.

Applying the experience gained from observations on Lake Mendota, it may fairly be assumed that Seneca Lake receives about 65,000 cal./cm.^{2} of surface during the period of the summer heat income. The lake loses, therefore, about one-half of the incident heat.

If we apply the mean sun data of Table 12 to this gross income, the sun delivers during this period about 13,400 cal. to the depth of 1 m.; 3,000 to 5 m.; and 450 to 10 m. These numbers are, respectively, 41 per cent, 11 per cent, and 1.9 per cent of the quantity of heat which passes through these levels. (See Table 7 for quantity of heat.)

The work attributed to the wind at these depths would be diminished by the aid of the sun in the same ratio that the heat delivered by the sun bears to the total amount of heat passing through those levels. Computed on this basis, the sun does all of the work of distributing heat at the surface, 41 per cent at 1 m. depth, 11 per cent at 5 m., etc. These quantities may be plotted as on figure 3 (p. 229) and the points connected by a curve. Then the area *ODBO* is proportional to the total work done by the sun under the conditions assumed. This area may be measured with a planimeter. It is equal to about 16 per cent of the area representing the total work. The part of it below 1 m. is about 10.9 per cent of the work done below 1 m. of depth.

This represents the maximum possible aid which, under the conditions assumed, the sun can give in the distribution of heat, for it assumes that the entire loss of incident radiation by the lake, amounting to one-half of that received, falls on the wind-placed heat and that no loss falls on the sun-placed heat. This assumption is evidently not correct. If, instead, we assume that the sun-placed heat suffers equal losses with that distributed by the wind, the aid of the sun will be reduced to about 8 per cent of the total work done and to about 5.5 per cent of the work done below 1 m.

Probably the assumption of equal losses is unfair to the sun. A great part of the lost heat is in that which is absorbed by the thin stratum at the surface and is used in evaporation, lost to the air at once or during the following night, etc. Almost all of the heat in the longer waves of the spectrum is absorbed by a much thinner layer of water than 1 m. Schmidt (1908, p. 240) computes that about 27 per cent of the solar energy is absorbed by 1 cm. of pure water and about 45 per cent by 1 dm. He uses Langley's energy curve for the solar spectrum, which makes his figures somewhat larger than would be the case in a curve for moderately high sun. In the curve which we have used as standard (path of rays equals 1.5 atmospheres) about 43 per cent of the energy would be absorbed by 25 cm. of pure water and 49 per cent by 50 cm. While no great accuracy can be claimed for the figures shown by Seneca Lake of about 67 per cent absorption for 25 cm. and 72 per cent for 50 cm., they are probably not greatly in error. The differences between them and the data for pure water are much the same as for greater depths. Thus more than one-half of the sun's energy is delivered to the upper centimeters of water from which loss to the air is easy. But much of the heat so delivered is distributed by the wind from the surface strata to deeper water, especially in the early part of the warming season when the lake is gaining heat rapidly. From this source comes the greater part of the heat which the lake gains below 1 m. in excess of that delivered by the sun. This heat amounts to 19,000 cal./cm.^{2} and much of it must come from the 40,000 cal./cm.^{2}, or more, absorbed by the upper 25 cm. of the lake. During bright and windy days there must be thus moved down into the lake by the wind much heat which is lost during cool periods when the whole upper water of the lake cools down.

It is true that on the whole the heat delivered by the sun to strata below the surface is more likely to be retained, as the water above a stratum must be cooled to a lower temperature than the deeper water before any heat can be lost by the latter. But several times each season there is a general cooling of the upper water, when much heat is lost, that placed by the sun as well as that placed by wind.

At present, therefore, no accurate estimate can be made of the loss of sun-placed heat at various depths. The subject must be left here with the general statement that between 84 and 92 per cent of the work done in distributing heat through the water of Seneca Lake is performed by the wind, on the assumption that conditions of transparency, etc., on August 1 were average ones. The amount really attributable to the sun is probably as much as 10 to 12 per cent. More than this can not be said, both in view of considerations presented above, and also in view of one other consideration which the study of Lake Mendota has shown. In the early part of the warming period, when gains of heat are rapid and when the deeper water is securing most of its heat, the sun plays a small part in distributing the heat. Later in the summer the sun has a much larger share of the work, when the epilimnion is forming, when gains of heat are small (perhaps only 5 to 10 per cent of the incident radiation), and when these gains are confined to the surface strata.

The foregoing paragraphs have dealt with Seneca Lake alone. The same methods may be applied to the other lakes with similar results. It is unnecessary to give the details of the computations; the results are shown in Table 16 (p. 235) and figures 4 and 5 (pp. 230, 231).

TABLE 16.—DIVISION OF DISTRIBUTION OF SUMMER HEAT INCOME BETWEEN SUN AND WIND IN THE LAKES AS A WHOLE AND IN THEIR SEVERAL STRATA. (See figs. 3, 4, 5, and text.)

[NOTE.—In this table, as elsewhere in this paper, "work" means the total work which would be needed to distribute the heat from the surface of the lake through the adjacent water, computed on the assumption that all heat is put into place by the wind mixing the warmer surface water with the cooler water below. In the division of the task of distributing heat between sun and wind it is also assumed that all losses of heat fall on wind-placed heat. This evidently attributes too large a share to the sun. Probably a fair estimate would be to allow to the sun all that it does below 1 m., i. e., about 10 to 11 per cent of the total.]

	Canandaigua Lake.		Cayuga Lake.		Seneca Lake.	
	Sun.	Wind.	Sun.	Wind.	Sun.	Wind.
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
Total work	16.9	83.1	15.0	85.0	15.8	84.2
Work, 0 to 5 m	31.6	68.4	33.1	66.9	32.0	68.0
Work, 5 to 10 m	2.9	97.1	4.6	95.4	6.6	93.4
Work, 0 to 1 m	62.3	37.7	60.8	39.2	58.3	51.7
Work, below 1 m	10.5	89.5	10.0	90.0	11.1	88.9
Work, below 5 m	1.7	98.3	2.4	97.6	3.3	96.7
Total work of sun and wind	1,929 g. cm.		2,446 g. cm.		2,874 g. cm.	

PLANKTON.

The fresh-water organisms which constitute what is known as the plankton may be separated into two groups, namely, (*a*) those forms which are large enough to be captured readily with a regular plankton net whose straining surface is made of bolting cloth, size No. 20 (new No. 25) and (*b*) those forms which are so small that they readily pass through the meshes of this bolting cloth. The former constitutes the net plankton and the latter may be called the nannoplankton. The latter term has been applied specifically to those organisms whose maximum diameter does not exceed 25 μ; but it is proposed to extend the meaning of this term to include all of the material that passes through the meshes of the net. The terms "macroplankton" and "microplankton" have been used to designate these two groups.

METHODS.

The net plankton was obtained by means of a closing net which has been fully described in a previous paper so that it is not necessary to consider it further here (Juday, 1916). The coefficient of this net is 1.2; that is, about 80 per cent of the column of water through which it is drawn is strained. The catches from the different strata were concentrated in the plankton bucket; the material was then transferred to 8-dram vials and preserved in alcohol. In the enumeration the volume of the catch was reduced to 10 cm.^{3}; after shaking thoroughly 2 cm.^{3} were removed with a piston pipette and the crustacea and rotifers contained therein were counted with a binocular microscope. The number thus obtained multiplied by the factor five represents the total of such organisms in the catch. When only a few of the larger crustacea were present, the total number was ascertained by direct count. The smaller organisms, such as the Protozoa and algæ, were enumerated by placing 1 cm.^{3} of the material in a Sedgwick-Rafter cell and ascertaining the number of the various forms in the usual manner by means of a compound microscope.

Samples of water for a study of the nannoplankton were obtained by means of a water bottle. The minute organisms were secured from these samples by means of an electric centrifuge having a speed of 3,600 revolutions per minute when carrying two

15 cm.^{3} tubes of water. The sedimentation was usually completed in about six minutes. The material was then transferred to a counting cell with a long pipette and the organisms were enumerated with a compound microscope having a 16 mm. objective and a No. 8 ocular. Many of these organisms, more especially the minute flagellates, are destroyed by the various preserving agents, so that it is necessary to have the living material for these enumerations; such counts must be made, therefore, as soon as possible after the samples of water are obtained.

The results obtained in the various enumerations are shown in Tables 17, 18, and 21. The figures indicate the number of individuals per cubic meter of water at the different depths. For purposes of comparison the results obtained for net plankton on Canandaigua, Cayuga, and Seneca Lakes in 1910 are shown in Table 18. Observations were made on the net plankton and nannoplankton of Green Lake, Wis., in 1918, soon after these were made on the Finger Lakes, and these have been included in Tables 17 and 21 for comparative purposes also.

NET PLANKTON.

Phytoplankton.—Table 17 shows that the green and blue-green algæ were scarce in the three Finger Lakes at the time of the observations in 1918. Only three forms were present, namely, Anabaena, Microcystis, and Staurastrum. In Canandaigua Lake a relatively small number of colonies of Microcystis was found in the upper 10 m. and Staurastrum was noted in the 10 to 40 m. stratum. In Cayuga Lake Anabaena was obtained in the upper 5 m. and Microcystis in the upper 10 m. In Seneca Lake this group was represented only by a few colonies of Microcystis in the 10 to 15 m. stratum. A comparison with Table 18 shows that fewer forms were present in 1918 than in 1910 and also that the number of individuals was much smaller in the former year. The two sets of catches on Canandaigua Lake present the most marked difference in this respect.

The net catches from Green Lake, Wis., contained a much larger algal population than the Finger Lakes, owing to the presence of a large number of filaments of Oscillatoria. This form was unusually well represented in the upper 15 m., a maximum of nearly two million filaments per cubic meter of water being found in the 0 to 5 m. stratum.

In the Finger Lakes the most abundant diatom, both in 1910 and 1918, was Asterionella, while Fragilaria was second in importance both years. In Canandaigua Lake the diatom population was substantially the same in these two years, while in Cayuga Lake the number was much larger in the former year. In Seneca Lake, on the other hand, the number was larger in 1918 than in 1910.

In Green Lake Asterionella was the only diatom noted, a few individuals of this form being present in two catches.

Zooplankton.—Uroglena was fairly abundant in the upper 30 m. of Canandaigua Lake and a few colonies of Epistylis were noted in the 5 to 10 m. stratum. In 1910 Ceratium was the most abundant protozoan in this lake; but it was not found in 1918.

In Cayuga Lake Actinosphaerium and Ceratium were about equally numerous in 1918, both being most abundant in the upper 15 m. The former was not found in 1910. and the latter was much more abundant in this year than in 1918, the number reaching more than a million and a half per cubic meter in the 0 to 5 m. stratum. Dinobryon was not as abundant in 1918 as in 1910 and Mallomonas was not noted in the former year.

In Seneca Lake Ceratium and Dinobryon constituted the protozoan population. A relatively small number of the latter was noted in the 5 to 10 m. stratum. Ceratium was distributed through the upper 20 m. but was most abundant in the upper 5 m.

The rotifer population was largest in Cayuga Lake and smallest in Canandaigua Lake in 1918. In the latter lake rotifers were most numerous in the upper 10 m. while in Cayuga and Seneca Lakes the largest number was found in the upper 15 m.

The maximum number of individuals in the rotifer group was noted for Synchaeta in Cayuga Lake, where it reached 44,700 per cubic meter of water in the 10 to 15 m. stratum; the average number in the upper 15 m. was 35,950 individuals. This form was not found in the other two lakes.

Polyarthra was noted in the catches from each of the three lakes in 1918, but it was most numerous in Cayuga Lake, reaching a maximum of 21,000 individuals per cubic meter in the 5 to 10 m. stratum. The maximum number in this lake in 1910 was a little more than ten times as large as this.

Conochilus was also found in the catches from each of the three lakes, but it, too, was most abundant in Cayuga Lake, reaching a maximum of 33,750 per cubic meter in the 0 to 5 m. stratum.

A few individuals of *Anuraea cochlearis* were found in the upper water of Canandaigua and Seneca Lakes, but this form also was distinctly more numerous in Cayuga Lake. The catches from Canandaigua Lake contained a few specimens of *Notholca longispina*, and the material from Cayuga Lake showed the presence of a few individuals of Asplanchna and Ploesoma in the upper water.

The rotifer population of Canandaigua Lake was substantially the same in 1918 as in 1910. (See Tables 17 and 18.) In Cayuga Lake Polyarthra was not nearly as abundant in 1918 as in 1910, but the other forms were more numerous, in general, in the former year. In Seneca Lake not so many forms were represented in 1918 as in 1910, but those that were present were more numerous, so that the total rotifer population was somewhat greater in the former year.

In Green Lake the rotifers were more abundant than in Canandaigua Lake, but they were not as numerous as in Cayuga Lake; the number in the upper 20 m. was substantially the same as that of this stratum in Seneca Lake.

Copepod nauplii were most abundant in the upper 20 m. or 30 m. of each lake, but they were present in the lower strata also. A larger number was found in Seneca Lake than in the other two lakes and the number in Seneca Lake was larger in 1918 than in 1910. In the other two lakes they were more numerous in the latter than in the former year. They were more abundant in Green Lake than in any of the Finger Lakes.

Three genera of copepods were represented in the net catches from each of the three Finger Lakes, namely, Cyclops, Diaptomus, and Limnocalanus; while a fourth, Epischura, appeared in the 5 to 10 m. stratum of Canandaigua Lake. By far the greater portion of the copepod population consisted of Cyclops and Diaptomus, the former being numerically greater than the latter in each of the lakes. Both of these forms were more abundant in Seneca Lake than in either of the other Finger Lakes. In the former the maximum number of Cyclops was 25,100 per cubic meter in the 0 to 5 m. stratum, with an average number of 21,460 in the upper 15 m. The maximum number of Diaptomus was 9,810 per cubic meter in the 15 to 20 m. stratum of Seneca Lake. Limnocalanus was present in the catches from each of the three Finger Lakes, but was confined to the deeper water.

In Canandaigua Lake the Copepoda were more numerous in 1910 than in 1918, but the reverse was true of the other two lakes.

The number of Diaptomus was larger in the upper strata of Green Lake than in any of the Finger Lakes, but Cyclops reached a larger number than in Seneca Lake only in the 0 to 5 m. stratum.

The Cladocera consisted of representatives of Sida, Diaphanosoma, Daphnia, Ceriodaphnia, and Bosmina. Bosmina was the most abundant form, and it was present in the water of Cayuga and Seneca Lakes in much larger numbers than in Canandaigua Lake. The maximum number obtained was 19,100 per cubic meter of water in the 10 to 15 m. stratum of Seneca Lake. The average number in the upper 15 m. of Cayuga and Seneca Lakes was 12,770 and 11,200 individuals per cubic meter, respectively.

Ceriodaphnia was found only in the 5 to 10 m. stratum of Cayuga Lake and Sida only in the 0 to 5 m. stratum of this lake. Diaphanosoma was noted only in the 0 to 5 m. stratum of Canandaigua Lake.

Daphnia retrocurva was obtained from the upper 30 m. of Canandaigua Lake, and a few young of this species were present in the 5 to 15 m. stratum of Cayuga Lake and in the 10 to 15 m. stratum of Seneca Lake.

In Canandaigua and Cayuga Lakes Cladocera were more abundant in 1910 than in 1918, while the reverse was true of Seneca Lake.

The Cladocera were more numerous in Green Lake than in Canandaigua Lake, but they did not reach as large a number as in Cayuga and Seneca Lakes.

The numerical data serve to give a reasonably accurate notion of the plankton population of these lakes, but such data alone do not give an adequate idea of the relative value of the various forms as a source of food for other organisms. When they are combined with data relating to the weights of the different organisms their value is very greatly enhanced. By means of small platinum crucibles and a sensitive assayer's balance the weights of the more important crustacean constituents of the plankton were obtained and the results of such determinations are shown in Table 19. Such data have also been secured for various constituents of the plankton of Wisconsin lakes and where such results were not obtained for some of the forms from the Finger Lakes, those from the former lakes have been used in computing the data shown in Table 20. The dry weight was obtained for all of the material and the wet weight as well for a few of the forms; after taking the dry weight the material was ignited in an electric furnace for the purpose of ascertaining the percentages of organic and inorganic matter.

In computing the data for crustacea in Table 20 the number of crustacea per cubic meter of water in a stratum was multiplied by the volume of that stratum and the total for the lake was ascertained by adding the numbers in the various strata. This total multiplied by the weight of the particular organism under consideration gave the amount of such material in the entire lake; this quantity divided by the surface area of the lake gave the weight per unit area, which is expressed in the table in kilograms and pounds per square kilometer and acre, respectively.

The amount of material per unit of surface is larger in the deep water than in the shallow water, but the sides of these lakes have such steep slopes that the results would not be altered very materially by taking this fact into consideration. Also it must be borne in mind that these figures are based upon a single set of catches in each lake and that a more extended series of observations might have yielded somewhat different results. The data in hand, however, are sufficient for a fairly good estimate. No organisms were weighed in 1910, but for purposes of comparison the data obtained in 1918 have been applied to the numerical results of the former year.

In 1910 Canandaigua Lake possessed the largest amount of crustacean material, having about 2,579 kg./km.^{2} of surface, while Seneca Lake was second with slightly more than three-quarters of this amount. Cayuga Lake, however, was less than 10 per cent below Seneca Lake. The greater portion of the material consisted of copepods in Canandaigua and Seneca Lakes; in the former they comprised about 67 per cent of the total amount of crustacean material and in the latter about 79 per cent.

In Cayuga Lake, however, about 72 per cent of the material consisted of the cladoceran Bosmina. Of the cladoceran material in Canandaigua Lake in 1910, *Daphnia retrocurva* furnished about 30 times as much as Bosmina and about 4 times as much as Diaphanosoma. Bosmina was the only representative of this group that was obtained from the other two Finger Lakes in 1910. Among the copepods Diaptomus was the most important form in this year and Cyclops ranked second.

In 1918 Canandaigua Lake possessed only about a third as much crustacean material as in 1910 and Cayuga Lake only about four-fifths as much. Seneca Lake, on the other hand, showed a much larger amount in the former year, the amount exceeding that of the latter year by about 62 per cent. Thus Seneca Lake in 1918 had almost four times as much crustacean material as Canandaigua Lake and more than twice as much as Cayuga Lake. *Daphnia retrocurva* was again the chief cladoceran element in Canandaigua Lake, but it was greatly exceeded by Bosmina in the other two lakes. Diaptomus furnished the largest amount of crustacean material in Canandaigua and Cayuga Lakes, but Cyclops was the chief constituent in Seneca Lake.

Green Lake, Wis., possessed a larger amount of crustacean material in 1918 than was found in the three Finger Lakes either in 1918 or in 1910. It was almost 10 per cent greater than that of Seneca Lake in 1918, which was the maximum for the three Finger Lakes. The copepods formed a much larger proportion of the material in Green Lake than in the Finger Lakes, because the Cladocera constituted a little less than 3 per cent of the total in this lake. Nearly two-thirds of the entire amount of crustacean material in Green Lake was furnished by Diaptomus.

Table 19 shows that the ash constitutes from 13 to 19 per cent of the dry weight of the crustacea of the Finger Lakes. In addition, also, it has been found that plankton crustacea contain from 4 to 9 per cent of chitin, which has no food value. In round numbers, then, it may be said that about 20 per cent of the dry weight of the plankton crustacea from the Finger Lakes consists of ash and chitin, while about 80 per cent may be regarded as actual food material. In the living state from 85 to 90 per cent of the mass of these organisms consists of water, so that the live weight would be approximately 10 times as large as the figures given in the dry weight column of Table 20, page 248.

In the crustacea from Green Lake the ash was much smaller, averaging somewhat less than 6 per cent; adding to this about 6 per cent for chitin leaves about 88 per cent of food material. The latter figure is higher than that for the Finger Lakes, which is due to the higher percentage of ash in the material from these lakes.

No determinations of the weight of the rotifers were made for the Finger Lakes, but such results have been obtained for three species from Wisconsin lakes, namely, *Asplanchna brightwellii*, *Brachionus pala*, and *Conochilus volvox*. The weight of these forms has been used as a basis for estimating the weight of the various rotifers in the plankton catches from the three Finger Lakes, N. Y., and from Green Lake, Wis. The computations are based on the relative volumes of the different forms, so that they are to be regarded as estimates and not the results of actual weighings. These estimates are shown in Table 20.

Cayuga Lake had the largest amount of rotifer material both in 1910 and in 1918, with 111 kg./km.^{2} (1 pound per acre) in the former year and 145 kg. (1.3 pounds) in the latter year. It had 4½ times as much as Seneca Lake in 1910 and about 3½ times as much in 1918; it had 12 times as much as Canandaigua Lake in 1910 and about 52 times as much in 1918. Green Lake had just half as much rotifer material as Cayuga Lake in 1918.

In the rotifers that have been weighed the ash averaged about 7.4 per cent of the dry weight, ranging from a minimum of a little less than 6 per cent to a maximum of a little more than 9 per cent. Thus between 90 and 95 per cent of the dry weight of these rotifers may be regarded as organic matter, but what proportion of this is indigestible has not been determined. Also it has been found that from 90 to 94 per cent of the living rotifer consists of water, so that the weight of the live organisms would be somewhat more than 10 times as large as the figures given in the table.

The relative importance of the crustacea and the rotifers as sources of organic matter which will serve as food for other organisms is shown in Table 20. In Canandaigua Lake, which had a very small rotifer population, the ratio of the organic matter in the rotifers to that in the crustacea was 1:256 in 1910 and 1:292 in 1918. Owing to the very much larger rotifer population in Cayuga Lake the ratio there was 1:13 in 1910 and about 1:9 in 1918. In Seneca Lake these ratios were about 1:70 each year. In Green Lake the crustacea contributed about 49 times as much dry organic matter as the rotifers in 1918.

The dry weight of the crustacea and rotifers combined amounted to 2,588 kg./km.^{2} (23 pounds per acre) in Canandaigua Lake in 1910; this was the maximum quantity found in the three Finger Lakes in that year. The minimum amount was noted for Cayuga Lake, namely, 1,945 kg. (17.3 pounds). (See Table 20, p. 248.)

In 1918 the maximum for these two groups of organisms was found in Seneca Lake and it amounted to 3,267 kg. of dry matter per square kilometer (29.1 pounds per acre). Canandaigua Lake possessed the minimum amount for this year, namely, about 852 kg. (7.6 pounds). This was only about one-third as much as this lake yielded in 1910.

In Green Lake these two groups of plankton animals yielded about 3,458 kg. of dry matter per square kilometer of surface (31.6 pounds per acre) which was about 10 per cent larger than the amount in Seneca Lake in 1918.

No attempt was made to determine the weight of the algæ in the net plankton, but as the catches appeared under the microscope by far the greater portion of the material consisted of rotifers and crustacea, probably three-quarters of it or more. Adding 25 or even 50 per cent to the above figures would still leave a relatively small amount of material per unit of surface. In general, these lakes may be regarded as poor in net plankton, the usual characteristic of lakes as large and as deep as these.

The figures given in the various tables represent the amount of material that is present on a particular date—that is, the standing crop at that time—but they do not indicate the quantity of such material that is produced annually. Production and destruction are processes which continue throughout the year, so that it is a very difficult problem to ascertain just how much net plankton is produced annually by a lake.

NANNOPLANKTON.

The nannoplankton includes the various forms of plants and animals which are so small that they readily pass through the meshes of the bolting-cloth strainer in the plankton net and are lost. These small organisms are easily obtained with a centrifuge. The results obtained in these enumerations on the three Finger Lakes of New York and on Green Lake, Wis., are shown in Table 21.

The Protozoa were represented by rhizopods, flagellates, and ciliates. The rhizopods consisted of Amoeba and some other forms which were not definitely identified. A minute Monas-like form was the most numerous flagellate found, while Cryptomonas was present in considerable numbers in Canandaigua and Seneca Lakes. A disk-shaped flagellate was noted in the upper strata of Cayuga and Green Lakes. Synura was also present in the surface stratum of Canandaigua Lake.

The only representative of the ciliates was Halteria. It appeared in the upper strata of Canandaigua and Cayuga Lakes.

The green and blue-green algæ consisted of Scenedesmus, Oocystis, and Aphanocapsa. A colonial form composed of very minute cells, 25 to 100 or more, embedded in a gelatinous matrix, has been referred to the genus Aphanocapsa. It appears to be widely distributed, geographically, since it has been found in all of the Wisconsin lakes from which nannoplankton has been obtained, and also in the three Finger Lakes. This alga has usually been fairly evenly distributed throughout the entire depth of the various lakes. This phytoplankton and the monads constitute the most common elements, numerically, of the nannoplankton.

The water bacteria belong to this group of plankton organisms, but they were not taken into consideration in these investigations.

No attempt was made to determine the amount of nannoplankton by weight, but some results that have been obtained on Lake Mendota, Wis., will serve as a basis for making a rough estimate for the Finger Lakes. The studies on Lake Mendota covered a period of more than two years and they consisted of both gravimetric and numerical determinations. The dry organic matter of the nannoplankton varied from a minimum of approximately 0.8 gr. to a maximum of 3.1 gr. per cubic meter of water. The numerical determinations which correspond most closely to those of the Finger Lakes average about 1.0 gr. of dry organic matter per cubic meter of water, so that this figure may be taken as a basis for estimating the amount of nannoplankton material in the latter. The results of this estimation are shown in Table 22, and also the results for total plankton. In the latter it has been assumed that the crustacea and rotifers furnished 75 per cent of the organic matter of the net plankton. Green Lake has not been included in this table because its net plankton contained a larger percentage of vegetable material.

These computations seem to indicate that the nannoplankton of Seneca Lake contained somewhat more than 2½ times as much dry organic matter as the net plankton, while in Canandaigua Lake the former was more than 4 times as great as the latter. These differences are of the same magnitude as those that have been obtained on Lake Mendota in midsummer. On an average, also, it may be considered that this material weighs at least 10 times as much in the living state, since most of these organisms, when alive, are made up of 90 per cent or more of water.

The results shown in this table represent only a single phase of the annual cycle, and hence they do not give any indication of the yearly production of such material. This latter question involves the actual turnover in stock each year and includes the various relations of the organisms to each other and to their environment; the chief phases of this question are the rate of reproduction of the various forms at different seasons of the year, and the relations of the consumers and their foods. The whole problem is very complex and would require an extended investigation for an adequate solution.

These quantities of dry organic matter in the total plankton of the Finger Lakes are very much smaller than those that have been obtained for Lake Mendota, Wis., in midsummer. In this latter lake the average amount for the month of July in 1915 and in 1916 was 40,630 kg./km.^{2} of surface (362.4 pounds per acre) in that portion of the lake having a depth of 20 m. or more; the average for August of these same years was 31,560 kg. (281.5 pounds). The average for Lake Mendota in July is more than three times the amount shown in this table for Seneca Lake and more than eight times that for Canandaigua Lake.

Comparisons have been made between the productivity of the land and of the water, but such comparisons have been based upon the production of beef on the one hand and of fish, or oysters, or other edible aquatic forms on the other hand. These materials are what may be termed the "finished products," and statistics relating to them give no idea of the relative amounts of food required or available for their production. This is accounted for by the fact that data concerning the quantity of food available, either directly or indirectly, for aquatic organisms have been for the most part wholly lacking and at best only fragmentary in character.

The quantitative results given above for the plankton, however, enable one to make direct comparisons with the land on material which is not an end product. The grass produced by a pasture is probably the best land crop for such a comparison, because it is less subject to artificial conditions resulting from cultivation than the grain crops. Henry (1898, p. 180) cites an experiment in which a pasture consisting of blue grass and white clover yielded 165,827 kg. of dry organic matter per square kilometer (1,477 pounds per acre) between May 1 and October 15. This quantity is just a little more than four times the average amount of organic matter maintained by the deeper water of Lake Mendota in July. In other words, a fourfold turnover in the stock of plankton maintained by Lake Mendota during this month would have yielded as much organic material annually as the pasture in the above experiment. During the vernal and autumnal maxima of the plankton the difference is distinctly less than fourfold. The roots were not included in this yield of grass and, taking them into consideration, we may say that the average difference for the year would be substantially fourfold. The differences are much greater in the Finger Lakes, ranging from about fourteenfold in Seneca Lake to almost thirty-fivefold in Canandaigua lake. (See Table 22, p. 250.)

The dry organic matter of the grass was made up of about 25.4 per cent crude protein, 4.7 per cent ether extract, while the remainder consisted of carbohydrates. The plankton of Lake Mendota, however, was distinctly richer in nitrogenous material and in fats; the average for the crude protein was 45.1 per cent of the dry organic matter and for the ether extract 8 per cent.

Attention should also be called to the fact that the plankton does not represent all of the food material that is produced by a lake; the bottom fauna and the large aquatic plants growing in the shallower water make notable contributions to this material. The quantity of plankton is not as large per unit of surface in the shallower water as it is in the deeper water, but the larger bottom population in the former region tends to counterbalance this deficiency when the question of the total production is considered.

PLANKTON TABLES.

Tables 17 and 18 show the vertical distribution of the various organisms constituting the net plankton, giving the number of individuals per cubic meter of water in the different strata. The members grouped in the different columns are indicated as follows:

CLADOCERA.—B=Bosmina, C=Ceriodaphnia, D=Daphnia, Di=Diaphanosoma, L=Leptodora, P=Polyphemus.

COPEPODA.—C=Cyclops, D=Diaptomus, E=Epischura, L=Limnocalanus.

NAUPLII.

ROTIFERA.—A=Asplanchna, A.a.=*Anuraea aculeata*, A.c.=*Anuraea cochlearis*, C=Conochilus, N=Notholca, P=Polyarthra, Pl=Ploesoma, R=Rattulus, S=Synchaeta, T=Triarthra.

PROTOZOA.—A=Actinosphaerium, C=Ceratium, D=Dinobryon, E=Epistylis, M=Mallomonas, U=Uroglena, V=Vorticella.

GREEN AND BLUE-GREEN ALGÆ.—An=Anabaena, Ap=Aphanocapsa, Coe=Coelosphaerium, G=Gloeocapsa, L=Lyngbya, M=Microcystis, O=Oscillatoria, S=Staurastrum.

DIATOMS.—A=Asterionella, F=Fragilaria, M=Melosira, S=Synedra, T=Tabellaria.

TABLE 17.—ANALYSIS OF NET PLANKTON, 1918.

CANANDAIGUA LAKE, JULY 27, 1918.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0-5	B 785 D 655 Di 785	C 1,310 D 1,830	13,470	A. c. 130 C 785 P 525	U 13,600	M 13,600	F 6,800
5-10	B 390 D 130	C 525 D 2,880 E 130	2,485	C 2,485 N 260	E 130 U 13,600	M 20,400	A 6,800
10-20	B 200 D 130	D 2,100 L 195	330	N 390	U 17,000	S 10,200	A 54,400 F 3,400
20-30	B 260 D 65	D 530 L 325	65	N 325 P 65	U 20,400	S 3,400	A 27,200
30-40	B 195	D 260 L 525	65	N 65	U 3,400	S 3,400	A 10,200
40-60		D 625 L 130	100		U 1,700		A 5,100
60-72		C 55 D 1,350 L 165	55				A 2,800

TABLE 17.—ANALYSIS OF NET PLANKTON, 1918—Continued.

CAYUGA LAKE, JULY 30, 1918.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0–5	B 10,200 S 130	C 7,200 D 260	2,485	A 915 A. c. 2,880 C 33,750 P 17,400 Pl. 150 S 25,770	A 108.800 C 129,200	An 13,600 M 6,800	A 13,600 F 20,400
5–10	B 14,250 C 130 D 130	C 915 D 1,700	2,880	A 1,180 A. c. 4,580 C 17,265 P 21,000 Pl. 300 S 37,400	A 34,000 C 102,000 D 6,800	M 6,800	A 27,200 F 27,200
10–15	B 13,865 D 130	C 650 D 4,580	3,800	A. c. 3,530 C 5,500 P 10,850 S 44,700	A 204,000 C 40,800 D 13,600		A 40,800 F 6,800
15–20	B 1,050	C 390 D 130	3,140	A. c. 390 C 260 P 1,960 S 2,350	A 13,600		A 6,800
20–30	B 130	C 1,635 D 1,960	3,990	A. c. 65 C 130 P 2,420 S 520			
30–50	B 65	C 2,500 D 1,520	790	A. c. 165 C 230 P 1,250 S 790	A 3,400 C 5,100		A 1,700 T 1,700
50–75	B 25	C 240 D 820 L 32	500	A. c. 50 C 50 P 340 S 105			A 1,360
75–100	B 25	C 50 D 160 L 32	80	A. c. 25 C 25 P 290 S 50	C 1,360		F 1,360

SENECA LAKE, AUG. 1, 1918.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0–5	B 6,500	C 25,100 D 3,800	12,700	A. c. 900 C 4,300 P 11,800	C 129,200		A 353,600 T 13,600
5–10	B 8,000	C 21,100 D 4,700	22,000	A. c. 400 C 400 P 6,700	C 47,600 D 6,800		A 272,000 T 6,800
10–15	B 19,100 D 260	C 18,180 D 6,800	19,100	A. c. 130 C 260 P 9,550	C 13,600	M 6,800	A 272,000 T 6,800
15–20	B 11,500	C 8,370 D 9,810	23,940	P 7,720	C 6,800		A 306,000
20–30	B 260	C 1,045 D 6,345 L 40	4,970	P 390			A 10,200
30–50	B 33	C 66 D 1,180 L 46	10,200	P 230			A 1,700
50–75		D 160 L 16	2,560	P 210			
75–100		D 26 L 5	55	P 55			A 1,300
100–125		C 26 D 26 L 5	53				
125–150		C 26 D 26 L 10	26	P 53			
150–170		C 132 D 33 L 13	230	P 66			A 800

TABLE 17.—ANALYSIS OF NET PLANKTON, 1918—Continued.

GREEN LAKE, WIS., AUG. 20, 1918.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0–5	B 1,570 D 392 Di 915	C 26,550 D 33,225	87,900	C 5,100 N 3,140 P 5,495	C 20,400 D 6,800	An 27,200 O 1,822,400	
5–10	B 260 D 525 Di 130	C 8,765 D 21,715	36,360	C 4,970 N 1,310 P 7,325	C 13,600	An 13,600 O 510,000	
10–15	B 130 D 1,440	C 6,280 D 4,055	3,530	A. c. 260 C 2,095 N 1,310 P 2,485	C 6,800	An 6,800 O 387,600	
15–20	D 655	C 785 D 1,180	14,260	A. c. 10,725 C 915 N 525 P 130 T 260		O 136,000	A 6,800
20–30	D 65	C 195 D 2,160	3,660	A. c. 4,250 C 130 N 65 P 130 T 520	D 3,400	O 142,800	
30–40	D 65	D 1,245 L 118	195	A. c. 110 N 65 T 460		An 6,800 O 173,400	
40–50	D 65	D 1,440 L 365	195	A. c. 720 C 130 T 260		An 3,400 O 85,000	
50–65	B 45	C 90 D 1,270 L 175	45	A. a. 45 A. c. 615 C 45 N 90 P 45 T 220		O 68,800	

TABLE 18.—ANALYSIS OF NET PLANKTON, 1910.

CANANDAIGUA LAKE, AUG. 20, 1910.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0–5	B 260 D 920 Di 3, 270	C 4, 500 D 14, 200	18, 500	C 130 P 1, 300	C 23, 200	Ap 11, 600 M 61, 900 S 3, 800	A 34, 800 F 3, 800
5–10	B 260 D 1, 600 Di 2, 500	C 3, 700 D 7, 200	5, 900	C 130 P 2, 100	C 92, 900	Ap 11, 600 Coe 3, 800 M 58, 000	A 34, 800 F 200
10–15	B 260 D 1, 300 Di 2, 750	C 2, 400 D 7, 600	2, 150	C 520 N 130 P 650	C 50, 300 D 7, 700	Ap 3, 800 Coe 23, 600 M 54, 200	A 50, 300 T 3, 800
15–20	B 130 D 130 Di 260	D 4, 190	390	C 520 P 200	C 3, 800	An 7, 700 Ap 7, 700 Coe 42, 600 M 15, 500	A 2, 100 T 1, 200
20–30	B 100 D 2, 230 L 30	D 1, 640 L 460		N 130	C 3, 800	An 1, 900 Ap 7, 700 Coe 7, 700 M 7, 700	
30–40	B 200 D 590	D 400 L 130	65	C 65 N 130	C 1, 900	Ap 1, 900 Coe 3, 800 M 1, 900	F 1, 900
40–60	B 230 D 25	D 360 L 100	25	C 130		Ap 2, 900 Coe 1, 900 M 2, 900	A 960 F 960 T 960
60–70	B 130	D 400 L 130		C 65 P 30	C 1, 900	Coe 3, 800 M 1, 900	
70–80	B 200	D 850 L 200			C 1, 900	Ap 1, 900 Coe 3, 800	

TABLE 18.—ANALYSIS OF NET PLANKTON, 1910—Continued.

CAYUGA LAKE, AUG. 12, 1910.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0–5	B 21, 500 C 260 P 130	C 1, 200	400	A 200 A. c. 520 P 239, 900 S 1, 000	C 1, 648, 600 D 15, 500 V 8, 800	A 9, 000 M 1, 000	A 2, 105, 300 F 812, 700 T 54, 200
5–10	B 32, 700 C 390	C 260 D 130	650	A 300 A. c. 650 P 38, 500 Pl 130 S 750	C 960, 000 D 15, 500 V 650	A 8, 000 M 7, 700	A 3, 204, 000 F 928, 800 T 108, 300
10–15	B 30, 500	C 520 D 1, 600	2, 500	A 170 A. c. 130 P 12, 600 Pl 1, 600 S 350	C 665, 600 D 15, 500 V 260	A 7, 700 M 31, 000	A 2, 182, 700 F 944, 300 T 123, 800
15–20	B 28, 000	C 260 D 2, 200	19, 200	A 140 A. a. 130 A. c. 3, 700 N 130 P 6, 000 Pl 910 S 250	C 270, 900 D 4, 000 M 116, 100	M 7, 700	A 1, 509, 000 F 611, 400 T 201, 000
20–30	B 2, 300	C 1, 400 D 790	4, 300	A 100 A. a. 130 A. c. 1, 580 N 80 P 60 Pl 60 S 200 T 460	C 73, 500 D 3, 900 M 31, 000	M 3, 900	A 569, 000 F 301, 800 T 104, 500
30–50	B 360	C 720 D 790	1, 200	A. a. 60 A. c. 130 N 150 P 2, 100 Pl 50 S 250 T 100	C 7, 600 M 1, 900	M 3, 500	A 67, 500 F 23, 100 M 3, 800 T 27, 000
50–75	B 80	C 640 D 340	1, 000	A. a. 25 A. c. 25 N 50 P 630 Pl 50 S 150 T 30	C 10, 800	M 1, 500	A 41, 800 F 7, 700 T 7, 700
75–100	B 670	C 80 D 20	60	A. c. 30 N 30 P 630 Pl 50 S 200 T 30	C 26, 300	M 1, 500	A 35, 600 F 20, 000 T 7, 700
100–120	B 60	C 50 D 100	160	A. c. 90 N 30 P 180 S 90 T 90	C 15, 000 M 1, 900	M 1, 500	A 30, 900 F 9, 600 T 15, 200

SENECA LAKE, AUG. 2, 1910.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
0–10	B 6,750 C 60	C 920 D 260	4,060	A 2,060 A. c. 2,100 N 60 P 2,300 Pl 1,450 R 50 S 2,000	C 32,800 D 1,900 V 60	An 1,900 M 7,700	A 135,000 F 17,300 M 1,900 T 7,700
10–20	B 8,060	C 4,200 D 1,300	9,500	A 50 A. c. 4,300 C 250 N 130 P 2,300 Pl 200 R 100 S 200	C 73,300 V 920	M 17,400	A 310,700 F 5,800 S 1,900 T 9,600

TABLE 18.—ANALYSIS OF NET PLANKTON, 1910—Continued.

SENECA LAKE, AUG. 2, 1910—Continued.

Depth in meters.	Cladocera.	Copepoda.	Nauplii.	Rotifera.	Protozoa.	Green and blue-green algæ.	Diatoms.
10–30	B 1,050	C 8,400 D 3,800	19,100	A 220 A. a. 220 A. c. 1,120 C 450 N 220 P 2,100 Pl 100 R 110	C 9,600 M 9,600	M 5,800	A 169,800 F 9,600 T 3,800
30–50	B 140	C 2,200 D 3,400	1,900	A. c. 200 P 280 S 30	C 500	M 1,000	A 3,400 F 1,000 T 500
50–75	B 25	C 50 D 820	2,000	A. c. 70 P 70	C 500	M 500	A 1,000 F 250 T 250
75–100	....	C 50 D 250 L 30	750	A. c. 30 P 130	C 250	M 700	A 250
100–130	....	C 40 D 100 L 20	280	A. c. 20 P 40	C 600	M 400	A 200
130–165	....	C 20 D 150 L 10	400	A. c. 20 P 40	C 170	M 850	A 100 F 500

TABLE 19.—WEIGHTS OF DIFFERENT FORMS OF CRUSTACEA FROM THREE FINGER LAKES, N. Y., AND FROM GREEN LAKE, WIS.

CANANDAIGUA LAKE.

Organism.		Wet weight in milligrams.		Dry weight in milligrams.		Per cent. of water.	Per cent. of ash.	Remarks.
Name.	No.	Total.	Each.	Total.	Each.			
Daphnia	54	....	....	1.25	0.0230	....	22.40	Adults.
Diaptomus	200	....	....	1.64	.0082	....	13.41	
Limnocalanus	150	....	....	5.14	.0343	....	5.45	Mixed sizes.
Mysis	20	....	....	22.20	1.1100	....	12.02	Do.
Bosmina	304	....	....	.90	.00296	....	31.11	Chiefly adults.
Polyphemus	77	....	....	.78	.0101	....	21.80	Mixed sizes.

CAYUGA LAKE.

Name.	No.	Wet weight Total.	Wet weight Each.	Dry weight Total.	Dry weight Each.	Per cent. of water.	Per cent. of ash.	Remarks.
Cyclops	404	....	....	1.89	0.0047	....	12.70	Chiefly adults.
Limnocalanus	250	....	....	12.75	.0510	....	3.78	Large.
Cyclops	532	23.46	0.0441	2.34	.0044	90.00	15.38	Chiefly adults.

SENECA LAKE.

Name.	No.	Wet weight Total.	Wet weight Each.	Dry weight Total.	Dry weight Each.	Per cent. of water.	Per cent. of ash.	Remarks.
Diaptomus	200	12.16	0.0608	1.26	0.0063	89.64	15.08	
Limnocalanus	108	37.77	.3497	5.14	.0476	86.40	6.61	
Daphnia	500	....	....	2.56	.0051	....	15.62	Mixed sizes.

GREEN LAKE.

Name.	No.	Wet weight Total.	Wet weight Each.	Dry weight Total.	Dry weight Each.	Per cent. of water.	Per cent. of ash.	Remarks.
Diaptomus	500	....	....	3.69	0.0074	....	5.15	Chiefly adults.
Limnocalanus	550	....	....	17.88	.0325	....	3.75	

TABLE 20.—DRY WEIGHT AND ORGANIC MATTER OF PLANKTON CRUSTACEA AND ROTIFERS IN THREE FINGER LAKES, N. Y., AND IN GREEN LAKE, WIS.

Organism.	1910				1918			
	Dry weight.		Organic matter.		Dry weight.		Organic matter.	
	Kilograms per square kilometer of surface.	Pounds per acre.	Kilograms per square kilometer of surface.	Pounds per acre.	Kilograms per square kilometer of surface.	Pounds per acre.	Kilograms per square kilometer of surface.	Pounds per acre.
CANANDAIGUA LAKE.								
Plankton crustacea:								
Bosmina	22.95	0.20	15.80	0.14	27.70	0.25	19.10	0.17
Daphnia	667.10	5.94	517.70	4.61	94.70	.84	73.50	.65
Diaphanosoma	165.00	1.47	154.70	1.38	16.30	.14	15.30	.13
Cyclops	209.22	1.86	182.60	1.62	38.50	.34	33.60	.30
Diaptomus	1,263.60	11.25	1,094.15	9.74	385.10	3.43	333.50	3.00
Limnocalanus	168.00	1.50	158.80	1.42	271.20	2.41	256.40	2.28
Epischura					10.10	.09	9.50	.08
Nauplii	83.00	.74	72.21	.64	5.30	.05	4.60	.04
Total	2,578.87	22.96	2,195.96	19.55	848.90	7.55	745.50	6.65
Rotifers	9.25	.08	8.56	.074	2.76	.024	2.55	.022
CAYUGA LAKE.								
Plankton crustacea:								
Bosmina	1,320.25	11.75	909.52	8.10	459.43	4.09	316.57	2.82
Daphnia					14.38	.13	11.20	.10
Cyclops	155.41	1.38	135.67	1.20	374.61	3.33	327.00	2.90
Diaptomus	255.42	2.27	221.16	1.97	519.00	4.60	449.40	4.00
Limnocalanus					36.13	.32	34.70	.28
Nauplii	103.06	.92	89.66	.80	68.00	.60	59.20	.52
Total	1,834.14	16.32	1,356.01	12.07	1,471.55	13.07	1,198.07	10.62
Rotifers	110.91	1.00	102.78	.92	145.24	1.30	134.50	1.20
SENECA LAKE.								
Plankton crustacea:								
Bosmina	418.57	3.72	288.40	2.56	421.00	3.75	290.00	2.60
Daphnia					16.70	.14	13.00	.10
Cyclops	631.28	5.62	534.19	4.75	1,491.60	13.30	1,262.00	11.30
Diaptomus	693.22	6.17	589.24	5.24	1,192.00	10.60	1,013.20	9.00
Limnocalanus	33.72	.30	31.50	.28	69.00	.61	64.40	.57
Nauplii	215.25	1.91	182.47	1.62	35.70	.32	30.30	.27
Total	1,992.04	17.72	1,625.80	14.45	3,226.00	28.72	2,672.90	23.84
Rotifers	24.58	.22	22.78	.20	41.28	.37	38.22	.34
GREEN LAKE.								
Plankton crustacea:								
Bosmina					24.00	0.21	22.44	0.20
Daphnia					59.35	.53	50.00	.44
Diaphanosoma					20.60	.18	19.30	.17
Cyclops					809.00	7.20	760.50	6.80
Diaptomus					2,034.31	18.10	1,929.54	17.16
Limnocalanus					104.20	.92	100.30	.88
Nauplii					424.00	3.77	400.68	3.55
Total					3,475.46	30.91	3,282.76	29.20
Rotifers					72.70	.65	67.32	.60

Table 21 shows the vertical distribution of the organisms in the nannoplankton, indicating the number of individuals per cubic meter of water at the different depths. The forms are as follows:

PROTOZOA—A=Amoeba, C=Cryptomonas, F=unidentified asymmetrical flagellate, H=Halteria, M=monads, R=unidentified rhizopods, S=Synura,

GREEN AND BLUE-GREEN ALGÆ—Ap=Aphanocapsa, Oo=Oocystis, Sc=Scenedesmus

DIATOMS—N=Navicula, S=Stephanodiscus, Sy=Synedra.

TABLE 21.—ANALYSIS OF NANNOPLANKTON.

CANANDAIGUA LAKE, JULY 28, 1918.

Depth in meters.	Protozoa.	Green and blue-green algæ.	Diatoms.	Depth in meters.	Protozoa.	Green and blue-green algæ.	Diatoms.
0	C 31,242,000	Ap 135,382,000	S 15,621,000	20	C 5,207,000	AP 98,933,000	N 10,414,000
	M 52,000,000				M 10,414,000		S 83,300,000
	S 5,200,000			39	M 31,242,000	Ap 130,175,000	N 10,414,000
5	C 10,414,000	Ap 182,245,000	S 36,449,000				S 88,520,000
	H 5,200,000		Sy 10,414,000	45	C 15,621,000	Ap 135,382,000	N 5,207,000
	M 15,621,000				M 15,621,000		S 10,414,000
10	C 5,207,000	Ap 187,452,000	S 31,242,000	60	C 5,207,000	Ap 130,175,000	S 26,035,000
	H 5,200,000		Sy 5,207,000		M 10,414,000		
	M 20,828,000			65		Ap 229,108,000	S 10,414,000
15	C 20,828,000	Ap 156,210,000	N 10,414,000				
	H 5,200,000	Sc 20,828,000	S 57,277,000				
	M 10,414,000						

CAYUGA LAKE, JULY 30, 1918.

0	F 31,242,000			20	M 20,828,000	Ap 62,484,000	S 5,207,000
	H 5,207,000	Ap 93,726,000	N 5,207,000	30	M 26,035,000	Ap 67,691,000	S 5,207,000
	M 26,035,000	Sc 20,828,000	S 5,207,000	50	M 26,035,000	Ap 52,070,000	S 5,207,000
	R 20,828,000			75	M 15,621,000	Ap 62,484,000	
5	F 26,035,000	Ap 62,484,000		100	M 10,414,000	Ap 67,691,000	S 5,207,000
	M 20,828,000	Sc 20,828,000	S 5,207,000		R 5,207,000		
	R 52,070,000						
10	C 5,207,000	Ap 78,105,000					
	M 36,449,000	Sc 10,414,000	S 5,207,000				
	R 20,828,000						

SENECA LAKE, AUG. 1, 1918.

0	C 41,656,000	Ap 72,898,000	S 15,621,000	30	C 5,207,000	Ap 36,449,000	
	M 145,800,000	Oo 5,207,000	Sy 5,207,000		M 36,449,000	Oo 10,414,000	S 10,414,000
5	C 15,621,000	Ap 161,417,000	S 15,621,000		R 5,207,000		
	M 119,761,000	Oo 10,414,000		50	M 20,828,000	Ap 62,484,000	S 5,207,000
10	C 5,207,000	Ap 62,484,000	S 15,621,000	75	M 5,207,000	Ap 72,898,000	S 10,414,000
	M 20,828,000	Oo 15,621,000		100	M 15,621,000	Ap 67,691,000	S 10,414,000
15	C 5,207,000	Ap 67,691,000	S 15,621,000	135	M 10,414,000	Ap 46,863,000	S 5,207,000
	M 10,414,000	Oo 26,035,000		170	M 5,207,000	Ap 67,691,000	S 5,207,000
20	C 5,207,000	Ap 36,449,000	S 10,414,000				
	M 10,414,000	Oo 10,414,000					

GREEN LAKE, WIS., AUG. 20, 1918.

0	F 5,207,000		S 5,207,000	20	M 20,828,000	Ap 72,900,000	S 5,207,000
	M 10,414,000	Ap 145,800,000	Sy 20,828,000		R 5,207,000		
	R 5,207,000			30	M 5,207,000	Ap 46,800,000	S 5,207,000
5	F 10,414,000	Ap 145,800,000	S 5,207,000	40	A 5,207,000	Ap 57,200,000	S 5,207,000
	M 10,414,000		Sy 15,621,000		R 5,207,000		Sy 5,207,000
10	F 15,621,000	Ap 130,200,000	S 5,207,000	50	M 5,207,000	Ap 67,700,000	S 10,414,000
	M 26,035,000		Sy 15,621,000	65	M 5,207,000	Ap 62,500,000	S 5,207,000
15	M 10,414,000	Ap 52,070,000	S 5,207,000				Sy 5,207,000

Table 22.—Estimates for Quantity of Nannoplankton and Total Plankton in Three Finger Lakes in 1918.

[Note.—Total plankton equals net plankton plus nannoplankton. Quantities are shown in kilograms of dry organic material per square kilometer of surface and pounds per acre. Living material would weigh about 10 times as much as is indicated in the table.]

Lake.	Nannoplankton.		Total plankton.	
	Kilograms per square kilometer.	Pounds per acre.	Kilograms per square kilometer.	Pounds per acre.
Canandaigua	3,877.3	34.5	4,809.2	42.8
Cayuga	5,450.0	48.5	6,947.5	61.6
Seneca	8,859.4	78.8	12,200.5	108.6

BOTTOM FAUNA.

Samples of the bottom at different depths were obtained in the three Finger Lakes and also in Green Lake by means of an Ekman dredge. This mud was sifted through a fine meshed net and the organisms found therein were enumerated. The dry weight and the ash of four of these bottom forms were ascertained. The results of these dredge hauls are shown in Table 23. The observations were far too few in number to give anything more than a fragmentary idea of the density of the bottom fauna, since only two hauls each were made in Canandaigua and Cayuga Lakes and but four in Seneca Lake; in addition to this they were taken only in the deeper water. Hundreds, or better still, thousands of observations, covering the bottom of each lake in various places from the shore line to the greatest depths and extending through the different seasons of the year, would be necessary to give an adequate idea of the character and abundance of their bottom fauna.

Only four forms have been included in the table because they constituted by far the greater portion of the material obtained. A few nematodes and an occasional ostracod and bivalve mollusk were noted in the shallower depths, but they were not present in sufficient numbers to obtain their weights.

A few larvæ of Protenthes were obtained in the 32 m. haul in Seneca Lake and in the 45 m. haul in Green Lake, but these were the only instances in which this larva was noted.

Chironomid larvæ were found in all of the hauls except the one made at 32 m. in Seneca Lake. They were most abundant in Cayuga Lake, where they constituted by far the most numerous form at a depth of 113 m. In the other three lakes, however, they formed only a minor element of the bottom population, both in numbers and in bulk. Earlier in the season they were probably more numerous, because many had undoubtedly transformed to the adult stage by the time these observations were made.

In Canandaigua and Seneca Lakes the relict amphipod Pontoporeia was second in importance, while it was third in Cayuga Lake and first in Green Lake. It was most abundant at a depth of 45 m. in Green Lake, where it furnished the largest amount of dry organic material that was found in any of the hauls, namely, about 8,214 kg./km.^{2}, or nearly 75 pounds per acre.

Oligochæta were found in all except one haul; that is, the one at 34 m. in Cayuga Lake. In half of the hauls they furnished the greater portion of the organic material.

The largest amount was obtained at 32 m. in Seneca Lake, where it reached 1,693 kg. of dry material per square kilometer, or a little more than 15 pounds per acre.

The deepest haul in Cayuga Lake yielded a larger amount of organic matter than the deepest haul in any of the other lakes, while the one at 34 m. was the poorest of all, due most probably to the fact that it was made on a very steep slope. Green Lake showed the second largest amount of material in its deepest water and Canandaigua Lake was third. In Seneca Lake the amount at 110 m. was only about three-quarters as great as at 172 m. In general, it appears that the bottom fauna in the deeper water of Green Lake yields a larger amount of dry organic matter per unit area than these three Finger Lakes.

TABLE 23.—NUMBER OF INDIVIDUALS AND WEIGHT OF BOTTOM FAUNA OBTAINED AT DIFFERENT DEPTHS IN THREE FINGER LAKES, N. Y., AND IN GREEN LAKE, WIS., IN 1918.

Depth in meters	Organism.	Number per square meter of bottom.	Dry weight.		Organic matter.	
			Kilograms per square kilometer.	Pounds per acre.	Kilograms per square kilometer.	Pounds per acre.
	CANANDAIGUA LAKE, JULY 28, 1918.					
20	Chironomus	800	219.2	1.95	155.0	1.38
	Pontoporeia	977	469.0	4.17	352.0	3.13
	Oligochaeta	1,420	522.9	4.65	459.1	4.08
74	Chironomus	45	12.0	.11	8.5	.07
	Pontoporeia	844	405.1	3.60	303.8	2.70
	Oligochaeta	890	326.8	2.91	286.9	2.55
	CAYUGA LAKE, JULY 30, 1918.					
34	Chironomus	133	36.4	.33	25.7	.23
	Pontoporeiia	178	85.4	.76	64.0	.57
113	Chironomus	3,863	1,058.5	9.42	784.4	6.66
	Pontoporeia	710	340.8	3.03	255.6	2.27
	Oligochaeta	1,288	474.0	4.22	416.2	3.70
	SENECA LAKE, AUG. 1, 1918.					
32	Protenthes	89	31.2	.28	28.8	.26
	Pontoporeia	1,110	532.8	4.74	399.6	3.55
	Oligochaeta	5,240	1,928.0	17.16	1,692.8	15.07
47	Chironomus	577	158.0	1.40	111.7	.99
	Pontoporeia	844	405.1	3.60	303.8	2.70
	Oligochaeta	1,330	489.4	4.35	429.7	3.82
110	Chironomus	444	120.6	1.07	85.3	.76
	Pontoporeia	355	170.4	1.52	127.8	1.14
	Oligochaeta	400	147.2	1.31	129.2	1.15
172	Chironomus	44	12.0	.11	8.5	.07
	Pontoporeia	133	63.8	.57	47.8	.43
	Oligochaeta	1,286	473.2	4.21	415.5	3.70
	GREEN LAKE, AUG. 20, 1918.					
45	Chironomus	59	27.7	.25	26.6	.24
	Protenthes	15	10.5	.09	9.7	.08
	Pontoporeia	6,882	9,910.0	88.26	8,213.6	74.93
	Oligochaeta	1,480	488.4	4.35	464.0	4.13
66	Chironomus	407	181.3	1.61	174.0	1.55
	Pontoporeia	459	661.0	5.90	561.2	5.00
	Oligochaeta	1,643	542.2	4.83	515.1	4.59

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DISTRIBUTION AND FOOD OF THE FISHES OF GREEN LAKE, WIS., IN SUMMER

By A. S. Pearse

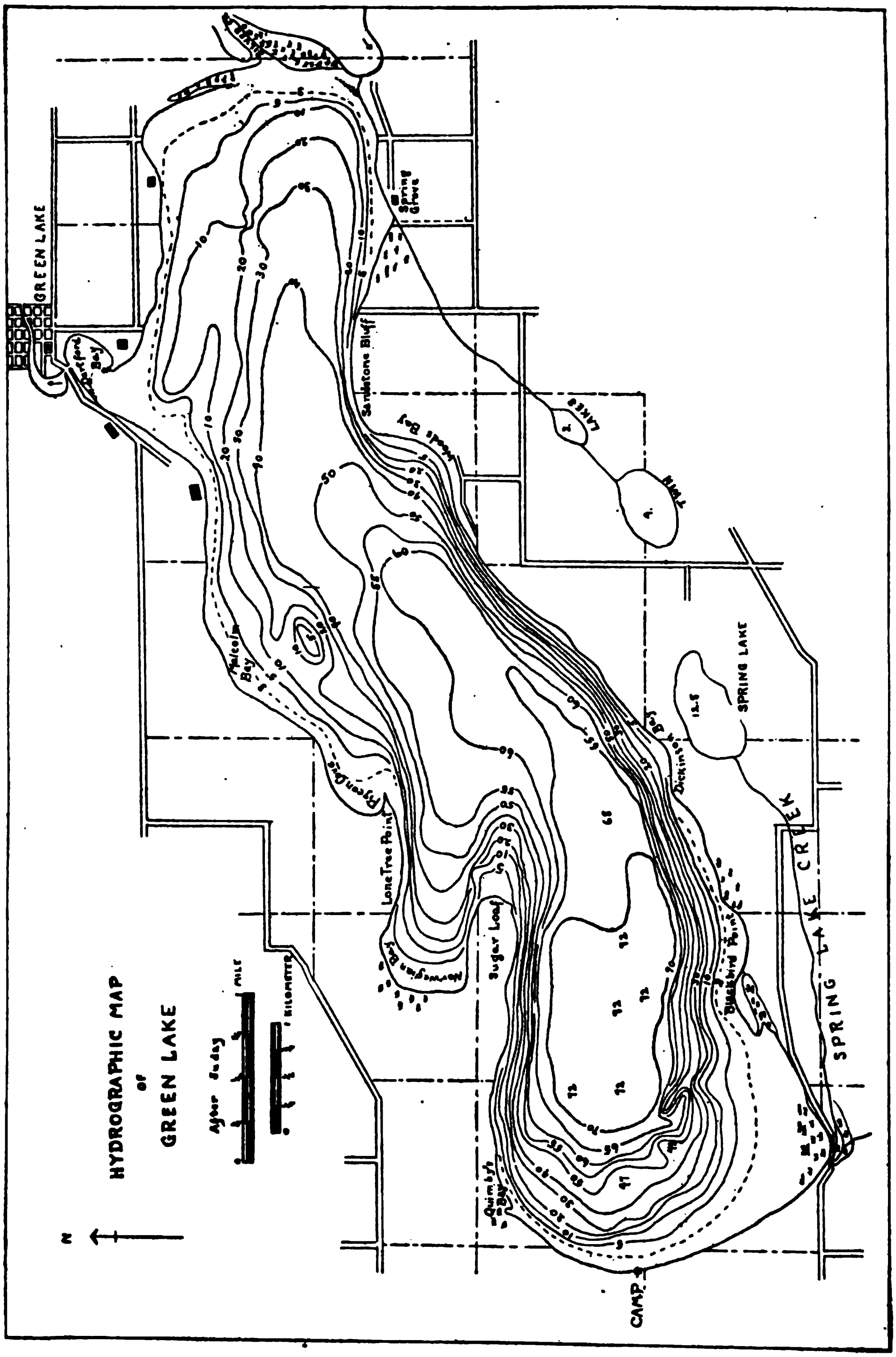
From BULLETIN OF THE BUREAU OF FISHERIES, Volume XXXVII, 1919–20

Document No. 906 : : : : : : : : : : : : : : : Issued October 7, 1921

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

PRICE, 5 CENTS
Sold only by the Superintendent of Documents, Government Printing Office, Washington, D. C.

WASHINGTON : : : : : : GOVERNMENT PRINTING OFFICE : : : : : : : : : : 1921



FRONTISPIECE.

DISTRIBUTION AND FOOD OF THE FISHES OF GREEN LAKE, WIS., IN SUMMER.

⁂

By A. S. PEARSE, *University of Wisconsin.*

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CONTENTS.

Page.
Introduction 255
Distribution of the fishes 256
Food of the fishes 262
General remarks on foods 266
Discussion and conclusions 270
Bibliography 272

INTRODUCTION.

Green Lake is of particular interest on account of its depth (237 feet). It measures 11.9 km. in length, 3.22 km. in width, has a maximum depth of 72.2 m., and a mean depth of 33.1 m. Its area at a depth of 70 m. is 2.1 km.[2] The water is very clear and the plankton content rather poor. The shores are for the most part sandy or stony, and the slope of the beaches is usually deep.

During the summer of 1919 the writer camped at the western end of the lake from August 11 to September 5. In front of the camp was a considerable stretch of sandy beach (frontispiece); the deepest parts of the lake and Spring Lake Creek (at the south-west corner of the lake) were readily accessible by rowboat. Temperatures were taken once each week and are recorded in Table 1.

TABLE 1.—TEMPERATURES OF GREEN LAKE IN DEGREES CENTIGRADE, 1919.[1]

Date.	Depth, in meters.									
	1	5	10	12.5	15	25	35	45	55	65
Aug. 14	22.2	22.2	16.4	9.5	8.1	6.4	5.7	5.2	5.0	4.9
Aug. 20	21.6	21.7	19.8	13.2	9.5	6.6	5.8	5.5	5.0	4.9
Aug. 28	21.2	20.7	20.6	12.6	9.1	6.0	6.0	5.8	5.0	4.9
Sept. 4	20.2	19.7	19.5	16.6	9.9	7.1	6.15	5.1	5.0	4.8

---

[1] The deep-sea thermometer used in taking the temperatures was loaned by C. Juday, of the Wisconsin Geological and Natural History Survey.

Fishing was carried on at various depths in the open lake and in Spring Lake Creek with gill nets measuring 75 by 4 feet. A 30 by 4 foot minnow seine was used in shallow water along the shores. Trot-lines baited with earthworms were set a few times, particularly to catch bullheads. Two hundred and three fishes, belonging to 17 species, were examined, special attention being given to the ciscoes, which were plentiful in deep water.

In making examinations the skin, fins, mouth, and gills first received attention. The fish was then slit open from vent to chin, and a careful inspection of the visceral organs was made. The contents of the intestine was stripped out on a glass plate and teased apart with needles under a binocular microscope, this being supplemented with a compound microscope when necessary. The intestine was then slit open and examined for food and parasites.

The data relating to parasites are reserved for a general publication dealing with several Wisconsin lakes; those concerning distribution and food are presented in this paper.

FISHES CAUGHT IN GREEN LAKE.

Ambloplites rupestris (Rafinesque): Rock bass.
Ameiurus natalis (Le Sueur): Yellow bullhead.
Ameiurus nebulosus (Le Sueur): Speckled bullhead.
Amia calva Linnaeus: Dogfish.
Boleosoma nigrum (Rafinesque): Johnny darter.
Catostomus commersonii (Lacépède): Common sucker.
Cyprinus carpio Linnaeus: German carp.
Esox lucius Linnaeus: Northern pike, pickerel.
Eupomotis gibbosus (Linnaeus): Pumpkinseed.
Fundulus diaphanus menona (Jordan and Copeland): Top-minnow.
Lepomis incisor (Cuvier and Valenciennes): Bluegill.
Leucichthys birgei Wagner: Cisco.
Micropterus dolomieu Lacépède: Smallmouth black bass.
Micropterus salmoides (Lacépède): Largemouth black bass.
Notropis atherinoides Rafinesque: Shiner.
Perca flavescens (Mitchill): Yellow perch.
Pimephales notatus (Rafinesque): Blunt-nosed minnow.

Other species doubtless occur in the lake. Joe Norton, an experienced fisherman living on the shore of the lake, says that gars are often seen. A sheepshead was caught in the lake several years ago.

DISTRIBUTION OF THE FISHES.

In order to determine the distribution of the fishes in Green Lake four methods were used. Gill nets were set at various depths; a minnow seine was used alongshore; trot-lines were set; and some trolling was done with a spoon hook.

The five gill nets used were always set tied together in a "string," all being of the same size (4 by 75 feet), but differing in the mesh (bar measure: ¾, 1, 1½, 2, 3 inches). Nets were set in the morning and pulled the following day. Table 2 gives a complete list of the catches in the string of gill nets.

TABLE 2.—GILL-NET CATCHES IN GREEN LAKE, 1919.[1]

Date.	Size of mesh.	Depth set.	Time set.	Catch.
	Inches.	*Meters.*	*Hours.*	
Aug. 13...	¾	41.5	22.5	3 ciscoes.
	1	41.5	22.5	14 ciscoes.
	1½	41.5	22.5	6 ciscoes.
	2	41.5	22.5	Nothing.
	3	41.5	22.5	2 ciscoes.
Aug. 14...	(2)	71.5	23.6	Nothing.
	1	71.5	23.6	8 ciscoes.
Aug. 15...	(3)	20	23.3	Nothing.
Aug. 16[4]..	¾	[6] 7.5	23.7	Nothing.
	1	[6] 8	23.5	1 rock bass.
	1	8	23.5	1 crayfish.
	1½	[5] 9.3	23.5	1 crayfish.
	2	[6] 12	23.5	2 pickerel.
	3	[6] 15	23	2 suckers.
	3	15	23	1 smallmouth black bass.
Aug. 18...	(2)	5	22	Nothing.
	1½	5	22	1 pickerel.
	1½	5	22	2 rock bass.
Aug. 19...	¾	70.3	24.2	2 ciscoes.
	1	70.3	24.2	68 ciscoes.
	1½	70.3	24.2	27 ciscoes.
	2	70.3	24.2	3 small ciscoes.
	3	70.3	24.2	1 small cisco.
Aug. 20...	(2)	50	23.5	Nothing.
	1	50	23.5	1 cisco.
	2	50	23.5	1 cisco.
Aug. 21...	(3)	37–44	23.3	Nothing.
Aug. 22...	(3)	21	22.7	Nothing.
Aug. 23...	(2)	8–10.5	23.5	Nothing.
	2	8–10.5	23.5	1 pickerel.
	3	8–10.5	23.5	1 smallmouth black bass.
Aug. 25...	(2)	2– 3.6	22.5	Nothing.
	¾	2– 3.6	22.5	5 perch.
	1½	2– 3.6	22.5	1 bluegill.
	1½	2– 3.6	22.5	1 pickerel.
	1½	2– 3.6	22.5	1 rock bass.
	2	2– 3.6	22.5	3 bluegills.
	2	2– 3.6	22.5	1 sucker.
Aug. 26...	¾	6	23.5	1 perch.
	1	6	23.5	1 centharcid.
	1½	6	23.5	1 pickerel, 1 rock bass.
	2	6	23.5	1 bluegill, 2 pickerel.
	3	6	23.5	Nothing.
Aug. 27...	(2)	3	23.7	Nothing.
	1	3	23.7	1 pickerel.
	1½	3	23.7	3 bluegills, 1 perch.
	1½	3	23.7	1 rock bass.
	2	3	23.7	1 pickerel.
Aug. 28...	¾	1.8	23.5	5 perch.
	1	1.8	23.5	2 pickerel.
	1½	1.8	23.5	4 pickerel.
	2	1.8	23.5	1 rock bass.
	3	1.8	23.5	Nothing.
Sept. 1[7]...	¾	1	7.6	1 pickerel, 1 pumpkinseed.
	1	1	7.7	4 perch, 9 pickerel.
	1	1	7.7	1 pumpkinseed.
	1½	1	7.2	1 bluegill, 3 perch.
	1½	1	7.2	12 pickerel.
	2	1	7.2	3 bluegills, 1 largemouth black bass.
	2	1	7.2	6 pumpkinseeds.
	3	1	6.8	Nothing.
Sept. 2....	¾	4	23.5	3 perch, 1 pickerel.
	1	4	23.5	1 pickerel.
	1½	4	23.5	1 pickerel, 1 carp.
	2	4	23.5	Nothing.
	3	4	23.5	Nothing.
Sept. 4....	¾	1.5–3	24.5	1 pickerel, 1 rock bass.
	1	1.5–3	24.5	1 rock bass.
	1½	1.5–3	24.5	1 pickerel, 1 rock bass.
	1½	1.5–3	24.5	1 clam (Lampsilis luteola).
	2	1.5–3	24.5	Nothing.
	3	1.5–3	24.5	Nothing.

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[1] All nets were 4 by 75 feet.

[2] Indicates that nets of the other meshes than those listed for catches on this date were set at the depth given, but nothing was caught.

[3] Indicates that five nets having ¾, 1, 1½, 2, and 3 inch meshes were set, but nothing was caught.

[4] Set string of nets on steep slope.

[5] Bare bottom.

[6] Among plants.

[7] Spring Lake Creek, half mile above mouth; set nets alternately from either bank, away from mouth, in following order: 3, 1½, ¾, 1, and 2 inch mesh.

Table 3 gives a summary of all the gill-net catches (except that of Sept. 1 in Spring Lake Creek) arranged according to depth.

This summary shows that ciscoes are confined to depths below 40 m. and the "catch per hour" figures indicate that ciscoes are the most abundant larger fishes in the lake. Young ciscoes probably spend a year or more in shallow water, for schools of from 100 to 200 fingerlings were observed three times, swimming in the middle of the lake at the surface in bright sunlight. The pickerel ranges deeper than other shallow-water species.

There is a zone above the ciscoes (20 to 40 m.) where there are few or no fishes. Footing up the "catch per hour" for all species at all depths we have the following figures: Total hours all nets were set—419.4; catch per hour—bluegills, 0.094; carp, 0.01; cisco, 1.447; largemouth black bass, 0; rock bass, 0.1; perch, 0.13; pickerel, 0.207; pumpkinseed, 0; smallmouth black bass, 0.03; sucker, 0.053.

If the abundance of fishes large enough to be caught in gill nets is judged by the "catch per hour," the species occur in the following ratios in Green Lake during the summer: Cisco, 48; pickerel, 7; perch, 4; rock bass, 3; bluegill, 3; sucker, 2; smallmouth black bass, 1; carp, +; large mouth black bass,[1] +; pumpkinseed,[1] +. These figures probably are almost correct with two exceptions: There are doubtless schools of carp too large to be caught in the nets used; and the pickerel, because it is fairly abundant and probably moves about more in search of food, is captured more often than the other fishes considered. There seems to be no question that the cisco is far more abundant than any other species.

TABLE 3.—SUMMARY OF GILL-NET CATCHES IN GREEN LAKE, 1919, GIVING DEPTH AND CATCH PER HOUR.

Depth in meters.	Size mesh in inches.	Time set in hours.	Blue-gill.	Rock bass.	Perch.	Pick-erel.	Carp.	Sucker.	Small-mouth black bass.	Cisco.
1 to 5	¾	117.5		0.01	0.11	0.01				
	1	117.5		.01		.04				
	1½	117.5	0.03	.02	.01	.06	0.01			
	2	117.5	.05	.01		.01		0.01		
	3	117.5								
Total			.08	.05	.12	.12	.01	.01		
5 to 10	¾	97.2			.01					
	1	97.2		.02					0.01	
	1½	97.2		.03		.02				
	2	69	.014			.044				
	3	69								
Total			.014	.05	.01	.064			.01	
10 to 20	¾	22.7								
	1	22.7								
	1½	22.7								
	2	46.2				.043				
	3	46.2						.043	.02	
20 to 40	¾	46.6								
	1	46.6								
	1½	46.6								
	2	46.6								
	3	46.6								
40 to 72	¾	93.8								0.053
	1	93.8								.98
	1½	93.8								.35
	2	93.8								.032
	3	93.8								.032
Total										1.447

It is interesting in this connection to compare the results for Lake Mendota during the summer of 1919. Lake Mendota has a maximum depth of 25.6 m. It differs from Green Lake ecologically in that its lower water stagnates (Birge and Juday, 1911). This means that the deeper parts (below 8 to 15 m.) are without oxygen during August, September, and October. The important ecological feature in this lake as a habitat for fishes is the fact that the water above the thermocline is well aerated and warm, while that below is without oxygen and comparatively cool. The temperatures of the water in Lake Mendota during the period work was being done in Green Lake are available through the courtesy of President E. A. Birge, of the University of Wisconsin.

While the writer was working in Green Lake, Leslie Tasche was setting a string of five nets (precisely like those used in Green Lake) in Lake Mendota. The summary of some of his catches will serve as a basis for comparison between the two lakes. The nets were set in Lake Mendota on the steep slope off the end of Picnic Point, where general conditions are much like those in Green Lake.

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[1] This species is included because young or adults were caught in the lake by other methods of fishing than gill nets; + indicates an amount less than 0.1 per cent. throughout this paper.

TABLE 4.—TEMPERATURES OF LAKE MENDOTA IN DEGREES CENTIGRADE, 1919.

Date.	Depth in meters.											
	0	5	8	9	10	11	12	13	15	17	20	23
Aug. 1	24.1	24.1	24.0	18.1	14.0	12.5	11.5	11.3	10.4	10.1	9.8	9.4
Aug. 19	23.3	22.6	22.4	22.3	16.3	12.7	11.6	10.9	10.4	10.1	9.8	9.7
Aug. 29	21.3	21.3	21.3	21.2	16.9	13.1	12.2	11.6	11.5	10.4	9.5	9.7
Sept. 4	20.3	20.3	20.2	20.2	18.5	15.7	12.8	12.2	10.8	10.2	10.0	10.0

FISHES CAUGHT IN GILL NETS IN LAKE MENDOTA.

Ambloplites rupestris (Rafinesque): Rock bass.
Catostomus commersonii (Lacépède): Common sucker.
Cyprinus carpio Linnæus: German carp.
Esox lucius Linnæus: Northern pike, pickerel.
Lepisosteus osseus (Linnæus): Gar.
Lepomis incisor (Cuvier and Valenciennes): Bluegill.
Leucichthys sp.?: Cisco.
Micropterus salmoides (Lacépède): Largemouth black bass.
Perca flavescens (Mitchill): Yellow perch.
Pomoxis sparoides (Lacépède): Crappie.
Roccus chrysops (Rafinesque): White bass.
Stizostedion vitreum (Mitchill): Wall-eyed pike.

TABLE 5.—GILL-NET CATCHES IN LAKE MENDOTA, 1919.[1]

Date.	Size mesh.	Depth set.	Time set.	Catch.
	Inches.	*Meters.*	*Hours.*	
June 24...	3/4	23	25	6 perch.
	1	23	25	55 perch.
	1 1/2	23	25	1 cisco.
	2	23	25	Nothing.
June 25...	(2)	21	23	Nothing.
June 26...	(3)	22	27.5	Nothing.
	1	22	27.5	1 perch.
July 28...	(2)	23	22.5	Nothing.
July 30...	(2)	22	22	Nothing.
Aug. 1....	3/4	19	24	Nothing.
	1	18	24	10 perch.
	1 1/2	16	24	1 cisco.
	2	15	24	Nothing.
	3	14	24	Nothing.
Aug. 2....	3/4	3	24	2 perch.
	1	4	24	1 gar, 14 perch, 1 rock bass.
	1 1/2	6	24	1 rock bass.
	2	9	24	Nothing.
	3	14	24	Nothing.
Aug. 7....	(3)	22	24	Nothing.
	1	22	24	1 perch.
Aug. 8....	3/4	13	23.5	9 perch.
	1	8	23.5	98 perch.
	1 1/2	7	23.5	3 rock bass.
	2	5	23.5	Nothing.
	3	4	23.5	Nothing.
Aug. 9....	3/4	13	25	19 perch.
	1	11	25	254 perch.
	1 1/2	9	25	3 rock bass.
	2	7	25	1 largemouth black bass.
	3	5	25	1 carp.
Aug. 12...	(3)	23	24	Nothing.
Aug. 13...	(2)	19-10	24	Nothing.
Aug. 14...	3/4	3	23.5	Nothing.
	1	4	23.5	22 perch.
	1 1/2	6	23.5	1 pickerel.
	2	8	23.5	1 carp.
	3	11	23.5	1 carp.
Aug. 19...	(3)	22	24	Nothing.
Aug. 20...	3/4	17	24	Nothing.
	1	14	24	12 perch.
	1 1/2	12	24	1 cisco.
	2	12	24	1 cisco.
	3	12	24	Nothing.
Aug. 21...	(3)	2-4	24	Nothing.
	1	2-4	24	1 crappie.
Aug. 22...	3/4	3	22.5	5 perch.
	1	3	22.5	2 perch, 1 rock bass.
	1 1/2	3	22.5	1 bluegill, 1 sucker.
	2	3	22.5	1 white bass.
	3	3	22.5	1 carp.
Aug. 23...	3/4	11	24.5	18 perch.
	1	7	24.5	111 perch.
	1 1/2	5	24.5	Nothing.
	2	4	24.5	1 wall-eyed pike.
	3	3	24.5	Nothing.
Aug. 26...	(3)	22	24	Nothing.
Aug. 27...	3/4	8	24.5	3 perch.
	1	6	24.5	1 largemouth black bass, 16 perch.
	1 1/2	5	24.5	Nothing.
	2	5	24.5	1 carp.
	3	4	24.5	3 carp.
Aug. 28...	3/4	16	22.5	Nothing.
	1	10	22.5	75 perch.
	1 1/2	6	22.5	1 rock bass, 1 white bass.
	2	4	22.5	Nothing.
	3	4	22.5	1 carp.
Aug. 29...	3/4	14	23.5	Nothing.
	1	13	23.5	8 perch.
	1 1/2	14	23.5	Nothing.
	2	12	23.5	Nothing.
	3	10	23.5	2 carp, 1 largemouth black bass.
Sept. 2....	(2)	22	23.5	Nothing.
Sept. 3....	3/4	7	23	9 perch.
	1	8	23	52 perch, 1 crayfish.
	1 1/2	10	23	1 cisco, 1 sucker.
	2	11	23	1 cisco.
	3	14	23	Nothing.
Sept. 4....	3/4	19	24	Nothing.
	1	18	24	1 perch.
	1 1/2	15	24	Nothing.
	2	12	24	1 carp.
	3	9	24	Nothing.
Sept. 5....	3/4	6	23.5	6 perch.
	1	7	23.5	1 crappie, 28 perch.
	1 1/2	7	23.5	1 crappie.
	2	8	23.5	Nothing.
	3	8	23.5	1 carp, 1 largemouth black bass.

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[1] All nets were 4 by 75 feet.

[2] Indicates that five nets, having 3/4, 1, 1 1/2, 2, and 3 inch meshes, were set, but nothing was caught.

[3] Indicates that nets of the other meshes than those listed for catches on this date were set at the depth given, but nothing was caught.

The data summarized in Table 5 cover a somewhat longer period of time than that including the catches in Green Lake. It might have been longer, for fishing in Lake Mendota was carried on from March 29 to September 29, 1919; but the general results do not differ markedly from those already published for this lake (Pearse and Achtenberg, 1920), and therefore only the period necessary to make adequate comparisons with Green Lake is listed. The summary shows clearly that perch were abundant in deep water in June and that they gradually migrated to higher levels as that region of the lake lost its oxygen. This migration offers a striking contrast to the conditions in Green Lake, where there is oxygen at all depths during the summer and where the common deep-water fishes (ciscoes) remain in the depths of the lake.

Table 6 gives a summary of catches in Lake Mendota from August 13 to September 4, grouped to show the total catches at different depths.

TABLE 6.—SUMMARY OF GILL-NET CATCHES IN LAKE MENDOTA, 1919, GIVING DEPTH AND CATCH PER HOUR.

Depth, in meters.	Size mesh, in inches.	Time set, in hours.	Perch.	Crappie.	Rock bass.	Bluegill.	Sucker.	Wall-eyed pike.	White bass.	Carp.	Largemouth black bass.	Cisco.	Pickerel.	Crayfish.
0 to 5	¾	70	0.07											
	1	70	.34	0.01	0.01									
	1½	95.5				0.01	0.01							
	2	118						0.01	0.01	0.01				
	3	142.5								.03				
Total.			.41	.01	.01	.01	.01	.01	.01	.04				
5 to 10	¾	47.5	.03											
	1	71	2.52								0.01			0.01
	1½	69			.01		.01		.04			0.01	0.01	
	2	23.5								.04				
	3	47.5								.04	.02			
Total.			2.55		.01		.01		.04	.08	.03	.01	.01	.01
10 to 15	¾	48	.38											
	1	48	1.36											
	1½	95.5										.01		
	2	116.5								.01		.02		
	3	94.5								.01				
Total.			1.74							.02		.03		
15 to 23	¾	166												
	1	119.5	.01											
	1½	71.5												
	2	71.5												
	3	71.5												
Total.			.01											

Footing the total catch per hour for all species caught in Lake Mendota the results are: Perch, 4.71; carp, 0.14; white bass, 0.05; cisco, 0.04; largemouth black bass, 0.03; rock bass, 0.02; sucker, 0.02; bluegill, 0.01; crappie, 0.01; pickerel, 0.01; wall-eyed pike, 0.01; gar, +; crayfish, 0.05. Most of the fishes were not caught below 10 m., the only exceptions being the carp, cisco, and perch.

The perch is by far the most abundant fish large enough to be caught in gill nets at all depths in Lake Mendota. The comparative number of fishes for the two lakes judged by catches per hour in gill nets, is shown in Table 7.

TABLE 7.—COMPARISON SHOWING RELATIVE NUMBERS OF FISHES IN GREEN LAKE AND LAKE MENDOTA, AS JUDGED BY CATCHES IN GILL NETS.

	Green Lake.	Lake Mendota.		Green Lake.	Lake Mendota.		Green Lake.	Lake Mendota.
Bluegill	9	1	Perch	12	471	Sucker	6	2
Carp	3	15	Pickerel	21	1	Wall-eyed pike		1
Cisco	144	4	Pumpkinseed	+	+	White bass		5
Crappie		1	Rock bass	9	2			
Gar	+	+	Smallmouth black bass	3	+	Total	186	506
Largemouth black bass	+	3						

This table shows that Green Lake does not have as many fishes large enough to be caught in gill nets as Lake Mendota. This is certainly true of the smaller fishes also, as judged by catches with minnow seines alongshore. The bearing of this fact will be discussed later. Table 7 also shows that there is an interesting compensatory relation between the fishes of the two lakes. The deep-water, bottom-feeding fishes—the perch in Mendota and the cisco in Green Lake—are much more abundant in both lakes than all the shallow water species together. The perch is absent from the deeper waters of Green Lake but in Mendota largely replaces the ciscoes in deep water and is more abundant than the pickerel, which exceeds it in Green Lake. The carp, crappie, largemouth black bass, wall-eyed pike, and white bass are more abundant in Lake Mendota. The bluegill, cisco, pickerel, rock bass, smallmouth black bass, and sucker are more abundant in Green Lake. It is interesting to note that the two fishes which probably are most similar in habits (the smallmouth and largemouth black bass) together have the same ratio of abundance in the two lakes. However, the smallmouth was the only one caught in gill nets in Green Lake and the largemouth the only one caught in Lake Mendota. These facts indicate that the two basses compete with each other and that peculiarities in the two lakes make each best fitted to one of them. In other words, there is room for a certain number of bass, and in Green Lake conditions are best suited for the smallmouth, in Lake Mendota for the largemouth.

The hauls for four days with the minnow seine are given in detail. These were made on a sandy beach bearing a scanty growth of aquatic plants at the west end of Green Lake from the shore line to a depth of 1½ m.

August 16.—Eighteen blunt-nosed minnows, 2 perch, 6 smallmouth black bass.

August 18.—Two largemouth black bass, 3 perch, 4 smallmouth black bass, 2 top minnows.

August 20.—Three Johnny darters, 2 largemouth black bass, 3 perch, 4 pickerel, 10 shiners, 10 smallmouth black bass, 3 top minnows.

August 29.—Four bluegills, 25 Johnny darters, 19 largemouth black bass, 17 perch, 1 pickerel, 1 shiner, 51 smallmouth black bass, 10 top minnows.

Summary.—Four bluegills, 18 blunt-nosed minnows, 28 Johnny darters, 23 largemouth black bass, 25 perch, 5 pickerel, 11 shiners, 71 smallmouth black bass, 15 top minnows.

Arranged in the order of their abundance, as judged by the catches in minnow seines, the small shore fishes rank as follows: Smallmouth black bass, 18; Johnny darter, 7; perch, 6.2; largemouth black bass, 5.8; blunt-nosed minnow, 4.5; top minnow, 3.7; shiner, 3; pickerel, 1.2; bluegill, 1.

These results again show the dominance of the smallmouth over the largemouth black bass in Green Lake, and (although the writer has not kept statistical records of hundreds of hauls) there is no doubt that the opposite is true in Lake Mendota. The Johnny darters are characteristic shallow-water fishes on sandy shores everywhere in Wisconsin. Some lakes, however, have other species of darters more abundant alongshore. For example, the Iowa darter (*Etheostoma iowæ*, Jordan and Meek) is the abundant one in Oconomowoc Lake. The minnows are characteristic more or less of all shallow-water habitats. The perch ranges through all bottom habitats and is probably the most versatile of our lake fishes. The pickerel, bass, and bluegill belong with the shore vegetation, and, as vegetation is not very plentiful in Green Lake, these fishes are not numerous.

On the evening (6.30 p. m.) of September 2, a trot-line 20 feet in length, bearing 49 No. 1 Limerick hooks baited with earthworms, was set outside a rush-grown bar extending from the bay behind Blackbird Point (front.) westward; depth, 1.2 to 2 m. Next morning (6.30 a. m.) the catch was 1 bluegill, 5 perch, 1 dogfish. At 6.50 p. m. on September 3, 50 hooks were set inside the same bar (1 to 1.5 m.) on 200 feet of line. The catch at 6.50 a. m. on September 4 was 7 bluegills, 4 perch, 1 rock bass, 1 mussel, *Lampsilis luteola* (Lamarck).

If these trot-line catches mean anything, they indicate that there are more bluegills inside the bar and that perch occur in equal numbers on either side. Perch, as has been suggested heretofore, are versatile fishes which invade practically all available habitats. Bluegills, though fitted to live among aquatic vegetation, are remarkably quick to take advantage of any new sources of abundant food. An instance of this was observed in Green Lake on the evening of August 22. The lake was very calm and on its surface were numerous ants, of some species that had been making its nuptial flight during that day. The whole surface of the west end of the lake was at intervals marked by little ripples caused by fishes feeding on the ants. All fishes observed from a rowboat before darkness fell were bluegills, though other species were doubtless taking advantage of this unusual supply of food.

FOOD OF THE FISHES.

The foods eaten by the fishes of Green Lake in 1919 are given in the following lists. The figures used in connection with foods all mean per cent by volume as estimated by the writer at the time of examination; + indicates an amount less than 0.1 per cent. Lengths of fishes are given in millimeters and do not include the caudal fin. Fishes are arranged in alphabetical order according to scientific names. Summaries for all species are given in Table 8. Unless otherwise mentioned all catches are off the sandy shore at the east end of the lake (frontispiece).

Ambloplites rupestris (Rafinesque). Rock bass.

August 16.—Depth, 8 m.; number examined, 1; length, 108. Food: Chironomid pupæ, 2; crayfish, 98.

August 22.—Number examined, 1; length, 30. Food: Chironomus larvæ, 25; mayfly larvæ, 50; Hyalella, 20; Eurycercus, 5.

August 23.—Number examined, 1; length, 47. Food: Chironomus larvæ, 5; large blue water mite, 30; ostracods, 2; cyclops, 12; Eurycercus, 3; Ceriodaphnia, 18; sand, 30.

August 26.—Number examined, 2; lengths, 192, 57. Food: Chironomus larvæ, 2.5; C. pupæ, 2.5; crayfish, 50; Ceriodaphnia, 45.5.

August 27, 28.—Number examined, 2; lengths, 190, 208. Food: Crayfish, 100.

September 4.—Number examined, 3; lengths, 213, 171, 111, average, 165. Food: Crayfish, 66.7; *Cambarus virilis*, 33.3.

Summary.—Number examined, 12 (2 empty); lengths, 30 to 213, average, 134. Food: Insect larvæ, 11.8; insect pupæ, 0.6; crayfishes, 64; mites, 4.2; ostracods, 0.2; amphipods, 2.9; entomostracans, 12; sand, 4.2.

Two-thirds of the food of this species consisted of crayfish.

Ameiurus natalis (Le Sueur). Yellow bullhead.

August 29.—Mouth of Spring Lake Creek; number examined, 2; lengths, 290, 270. Food: Fish, 32.5; mayfly nymphs, 10; insects, 17.5; Gelastocoris, 6.5; crayfish, 10; Hyalella, 12.5; Ceriodaphnia, 1; plants, 10.

Summary of food.—Fish, 32.5; insects and nymphs, 34; crayfishes, 10; amphipods, 12.5; entomostracans, 0.1; plants, 10.

A third of the food of this species was fish and a third insects.

Ameiurus nebulosus (Le Sueur). Speckled bullhead.

August 29, 1919.—Mouth of Spring Lake Creek; number examined, 9; lengths, 265 to 320, average, 302. Food: Mayfly nymphs, 2.8; dragonfly nymphs, 1; crayfish, 25.6; cladoceran, 0.1; amphipods, 0.8; Hyalella, 2.1; Sphæriidæ, 0.6; Planorbis, +; *Physa heterostropha*, 31.4; oligochætes, 3; *Herbobdella punctulata*, 4.2; seeds, 8.9; plants, 10.1; Myriophyllum, 3; filamentous algæ, 0.8; unknown débris, 5.6.

Summary of food.—Insect nymphs, 3.8; mites, 0.5; crayfishes, 25.6; amphipods, 2.6; cladoceran, 0.1; Sphæriidæ, 0.6; snails, 31.4; annelids, 7.2; plants, 22; algæ, 0.8; unknown, 5.6.

The favorite foods of this bullhead were snails, plants, and crayfishes.

Boleosoma nigrum (Rafinesque). Johnny darter.

August 20.—Number examined, 5; lengths, 32 to 46, average, 40.2. Food: Chironomus larvæ, 66; Hyalella, 10; ostracods, 0.2; sand, 23.8.

August 22.—Number examined, 1; length, 34. Food: Chironomus larvæ, 95; sand, 5.

August 24.—Number examined, 1; length, 38. Food: Chironomus larvæ, 75; sand, 25.

August 26.—Number examined, 4; lengths, 37 to 47, average, 41. Food: Chironomus larvæ, 92.5; sand, 7.5.

Summary.—Number examined, 11; average length, 38.3. Food: Chironomus larvæ, 82.1; amphipods, 2.5; ostracods, 0.1; sand, 15.3.

Catostomus commersonii (Lacépède). Common sucker.

August 16.—Depth, 14.5 m.; number examined, 2; lengths, 542, 510. Food: Chironomid larvæ, 23.5; Sialis nymph, 2.5; insects, 0.5; ostracods, 1; amphipods, 60; Eurycercus, +; oligochætes, 0.5; Sphæriidæ, 6.5; mud, 1; sedimentary débris, 4.5.

August 25.—Depth, 4 m.; number examined, 1; length, 364. Food: Chironomid larvæ, 4; Leptocella larva, 1; Hyalella, 2; Sphæriidæ, 76.8; Amnicola, 1; *Valvata tricarinata*, 0.2; sand, 15.

Summary.—Number examined, 3; lengths, 364 to 542, average, 445. Food: Insect and larvæ, 19.3; amphipods, 40.7; entomostracans, 0.7; clams, 29.9; snails, 0.4; oligochætes, 0.3; sedimentary débris, 3; mud and sand, 5.7.

The sucker partakes of a considerable variety of foods, the most important being amphipods, little clams, and insects.

Cyprinus carpio Linnaeus. German carp.

September 2.—Number examined, 1; length, 133. Food: Chironomid larvæ, 2; Hyalella, 25; ostracods, 33; Eurycercus, 1; Ceriodaphnia, 10; Sphæriidæ, 15; plant remains, 3; fine débris, 10; sand, 2.

Esox lucius Linnaeus. Pickerel.

August 16.—Depth, 11.5 m.; number examined, 2; lengths, 553, 576. Food: Shiners, 100.

August 18.—Depth, 5 m.; number examined, 2; lengths, 466, 410. Food: Minnows, 50; fish remains, 50.

August 20.—Number examined, 1; length, 402. Food: Fish remains, 70; ostracods, 10; Chara, 20.

August 22.—Number examined, 1; length 100. Food: Shiners, 100.

August 23.—Depths, 4.6, 11.5 m.; number examined, 2; lengths, 550, 495. Food: Perch, 25; shiners, 15; fish remains, 60.

August 26.—Number examined, 3; lengths, 570, 635, 665. Food: Fish remains, 100 (2 empty).

August 27.—Number examined, 2; lengths, 307, 565. Food: Fish remains, 100 (1 empty).

August 28.—Number examined, 5; lengths, 300 to 475, average, 393. Food: Minnows, 100 (3 empty).

September 2.—Number examined, 2; lengths, 485, 600. Food: Fish remains, 100 (1 empty).

September 3.—Number examined, 3; lengths, 211, 490, 540, average, 414. Food, Fish remains, 100 (1 empty).

Summary.—Number examined, 24; lengths, 100 to 665, average, 445. Food: Perch, 2.5; shiner, 21.5; minnow, 15; fish remains, 58; ostracods, 1; plants, 2.

Eupomotis gibbosus (Linnaeus). Pumpkinseed.

September 1.—Mouth of Spring Lake Creek; number examined, 4; lengths, 163 to 168, average, 165. Food: Chironomid larvæ, 2; dragonfly nymphs, 25; Planorbis, 33.3; Physa, 17.7; Valvata, 2; Sphæriidæ, 5; *Herbobdella punctulata*, 15.

September 2.—Near mouth of Spring Lake Creek; number examined, 1; length, 73. Food: Chironomid larvæ, 92; Sphæriidæ, 8.

Summary.—Number examined, 5; average length, 146. Food: Insect larvæ and nymphs, 59.5; snails, 26.5; small clams, 6.5; leeches, 7.5.

Fundulus diaphanus menona (Jordan and Copeland). Top minnow.

August 15.—Number examined, 1; length, 52. Food: Hyalella, 100.

August 18.—Number examined, 1; length, 52. Food: Chironomid larvæ, 60; chironomid pupæ, 19; gordiacean in chironomid pupæ, 1; sand, 20.

August 20.—Number examined, 2; lengths, 46, 59. Food, Chironomid larvæ, 10; chironomid pupæ, 15; Hyalella, 25; Ceriodaphnia, 25; Pleuroxus, 1.5; Bosmina, 10; Acroperus, 15; ostracods, 2.5; sand, 10.

August 21.—Number examined, 4; lengths, 50 to 53. Food: Chironomid larvæ, 11.3; chironomid pupæ, 23.8; Hyalella, 44.3; Ceriodaphnia, 14.3; Bosmina, 0.5; Chydorus, 1.5; ostracods, 0.5; sand, 4.

August 22.—Number examined, 1; length, 55; Food: Caddisfly larvæ, 45; Hyalella, 50; ostracods, 5.

August 23.—Number examined, 3; lengths, 18 to 53, average, 38. Food: Chironomid larvæ, 30; chironomid pupæ, 6.7; Hyalella, 20.2; Ceriodaphnia, 8.3; Chydorus, 6.7; ostracods, 23.3; sand, 5.

Summary.—Number examined, 12; lengths, 18 to 55, average, 44. Food: Chironomid larvæ, 17.9; caddisfly larvæ, 3.8; chironomid pupæ, 13.7; Hyalella, 31.8; cladocerans, 16.6; ostracods, 6.4; gordiacean, 0.1; sand, 5.9.

Lepomis incisor (Cuvier and Valenciennes). Bluegill.

August 25.—Number examined, 4; lengths, 164 to 186; average, 177. Food: Chironomid larvæ, 1.3; dragonfly nymphs, 0.3; *Leptocerus dilutus* larvæ and cases, 13.3; collembolan, +; ants, 8.8; mite, +; Hyalella, 66.7; Eurycercus, +; Amnicola, 0.3; Ancylus, +; plants, 1.5; algæ, 0.3; sand, 7.8.

August 26.—Number examined, 1; length, 176. Food: Chironomid pupæ, 0.2; Chara, 99.6; plants, 0.2.

August 27.—Number examined, 3; lengths, 143 to 170, average, 160. Food: *Leptocerus dilutus* larvæ and cases, 58.3; crayfish, 33.3; plants, 6.6; sand, 1.7.

August 29.—Spring Lake Creek; number examined, 1; length, 173. Food: Dragonfly nymphs, 15; insects, 40; seeds, 5; plants, 20; fine débris, 20.

August 30.—Number examined, 2; lengths, 43, 157. Food: Chironomid larvæ, 25; chironomid pupæ, 15; collembolan, 50; fine débris, 10.

September 1.—Spring Lake Creek; number examined, 1; length, 175. Food: Sponge, 10; Myriophyllum, 80; wild rice seeds, 10.

September 3.—Number examined, 1; length, 172. Food: *Melanoplus femur-rubrum*, 35; crayfish, 65.

September 4.—Number examined, 5; lengths, 164 to 188, average, 176. Food: *Leptocerus dilutus* larvæ and cases, 64.8; Physa, 1; Planorbis, 0.2; Potamogeton, 7; plants, 17.6; algæ, 6.

Summary.—Number examined, 18; lengths, 43 to 188, average, 165. Food: Insect larvæ, 33; insect pupæ, 1.7; adult insects, 12.9; mite, +; crayfishes, 9.2; amphiods, 14.8; cladocerans, +; snails, 0.5; sponge, 0.5; plants, 21.3; algæ, 1.7; fine débris, 2.2; sand, 2.2.

Leucichthys birgei Wagner. Cisco.

August 13.—Depth, 41.5 m.; number examined, 10; lengths, 148 to 288, average, 199. Food: Chironomid larvæ, 0.3; Mysis, 5; Pontoporeia, 76.6; copepods, 1.6; ostracods, 5; Sphæridæ, 11.1; Amnicola, 0.6; Planorbis, 0.2; brown, spindle-shaped seeds, 0.8; plants, 0.5; bottom ooze, 1.6; calcium carbonate crystals, 0.1; unknown, 1.1.

August 14.—Depth, 71.5 m.; number examined, 8; lengths, 207 to 246, average, 225. Food: Chironomid larvæ, 3.3; Mysis, 13.3; Pontoporeia, 24.2; Canthocamptus, 3.3; ostracods, 12.5; oligochætes, 21.7; Sphæriidæ, 0.8; brown seeds, 0.2; dandelion seed, 0.2; bottom ooze, 12.6.

August 19.—Depth, 70.5 m.; number examined, 12; lengths, 154 to 296, average, 228. Food: Chironomid larvæ, 0.2; Silais nymph, 0.4; Pontoporeia, 73; oligochætes, +; Sphæriidæ, 14.8; Valvata, 0.1; Linnæa, 0.2; Amnicola, 0.3; Planorbis, 0.6; brown seeds, 0.1; plants, 0.4; bottom ooze, 9.8.

Summary.—Number examined, 30; lengths, 148 to 296, average, 218. Food: Insect larvæ, 1.1; Mysis, 4.7; amphipodis, 61.2; copepods, 1.3; ostracods, 3; Sphæriidæ, 9.9; snails, 0.8; seeds, 0.4; plants, 0.3; bottom ooze, 8.2; calcium carbonate crystals, +; unknown, 0.3.

The cisco feeds largely on crustaceans and molluscs in summer. Eighty-eight per cent of its food is made of bottom ooze and the organisms associated with the bottom. Perhaps the ciscoes turn more to plankton at other seasons. If so, their feeding habits differ markedly from the perch, which is the deep-water fish in Lake Mendota, for it feeds largely from the bottom at all seasons (Pearse & Achtenberg, 1920).

Micropterus dolomieu Lacépède. Smallmouth black bass.

August 15.—Number examined, 6; lengths, 46 to 57, average, 51.5. Food: Chironomid larvæ, 6; Orthocladius, 30.1; mayfly nymphs, 0.6; chironomid pupæ, 4; insects, 0.8; Acroperus, +; Eurycercus, 0.1; Ceriodaphnia, 57.8; plant remains, 0.3; filamentous algæ, +; sand, 0.3.

August 16.—Depth, 14.5 m.; number examined, 1; length, 392. Food: Perch, 50; grasshopper, 50.

August 18.—Number examined, 2; lengths, 52, 56. Food: Chironomid larvaæ, 35; mayfly nymphs, 7.5; beetle larvæ, 5; chironomid pupæ, 30; Hyalella, 225.

August 21.—Number examined, 1; length, 55. Food: Chironomid larvæ, 35; Eurycercus, 1; Ceriodaphnia, 64.

August 23.—Depth, 10 m.; number examined, 1; length, 395. Food: Fish remains, 100.

Summary.—Number examined, 11; lengths, 46 to 395, average, 114. Food: Fish, 13.6; insect larvæ, 31.8; insect pupæ, 7.6; insect adults, 5; amphipods, 4.1; cladocerans, 37.6; plants, 0.2; sand, 2.

Micropterus salmoides (Lacépède). Largemouth black bass.

August 18.—Number examined, 3; lengths, 49, 58, 61. Food: Fish, 5; chironomid larvæ, 3.3; damselfly nymphs, 13.3; mayfly nymphs, 6.7; chironomid pupæ, 15.7; Corixa, 8.4; Chydorus, 0.3; amphipod, 2.7; Hyalella, 4; ostracods, 0.3; Eurycercus, 0.3; Ceriodaphnia, 39; sand, 1.

August 19.—Number examined, 1; length, 52. Food: Chironomid larvæ, 15; chironomid pupæ, 40; Eurycercus, 10; Ceriodaphnia, 30; sand, 5.

August 20.—Number examined, 1; length, 63. Food: Chironomid larvæ, 25; chironomid pupæ, 75.

August 21.—Number examined, 3; lengths, 63, 63, 64. Food: Chironomid larvæ, 6.7; mayfly nymphs, 5; chironomid pupæ, 9.3; fly, 3.3; Hyalella, 13.3; Ceriodaphnia, 61.3; sand, 1.

August 22.—Number examined, 8; lengths, 55 to 283, average, 97. Food: Chironomid larvæ, 9; mayfly nymphs, 6.3; chironomid pupæ, 13.5; midges, 14; fly, 0.3; crayfish, 8.1; Hyalella, 28.5; ostracods, 0.1; Chydorus, 0.1; Eurycercus, 0.8; Ceriodaphnia, 7.2; plants, 10.6; sand, 1.5.

Summary.—Number examined, 16; lengths, 49 to 283, average, 78. Food: Fish, 1; insect larvæ, 16.1; insect pupæ, 18.6; adult insects, 8; crayfish, 4; amphipods, 18; cladocerans, 24.8; ostracods, 0.1; plants, 5.2; sand, 1.4.

Only one of the fishes examined was over 88 mm. in length. This one had eaten chironomid pupæ, 15, and plants, 85. The most important foods for all bass examined are insects and their immature stages (42.7), cladocerans, and amphipods.

Notropis atherinoides Rafinesque. Shiner.

Only one shiner was examined for food and it was empty. It was supposed that shiners would be easy to catch alongshore and they were therefore neglected until the period for study was nearly completed—then none was to be found.

Perca flavescens (Mitchill). Yellow Perch.

August 15.—Number examined, 2; lengths, 68, 73. Food: Chironomus larvæ, 10; Orthocaldius larvæ, 15; mayfly nymphs, 2.5; caddisfly larvæ, 5; Hyalella, 15; ostracods, 0.5; Ceriodaphnia, 52.

August 18.—Number examined, 5; lengths, 70 to 113, average, 81. Food: Chironomid larvæ, 25; mayfly nymphs, 3; chironomid pupæ, 34; Hyalella, 12.4; Chydorus sphæricus, 0.2; Eurycercus, 1.2; Ceriodaphnia, 23.2; sand, 1.

August 22.—Number examined, 2; lengths, 93, 97. Food: Chironomid pupæ, 37.5; Hyalella, 59.5; Ceriodaphnia, 0.5; plants, 2.5.

August 23.—Number examined, 1; length, 74. Food: Chironomid larvæ, 22; caddisfly larvæ, 2; chironomid pupæ, 15; Hyalella, 32.8; Eurycercus, 23; Ceriodaphnia, 5; sand, 0.2.

August 25.—Number examined, 5; lengths, 115 to 127, average, 122. Food: Chironomid larvæ, 5; mayfly nymphs, 4; chironomid pupæ, 1; mite, 4; crayfish, 16.2; Hyalella, 19; ostracods, +; Physa, 39.6; Amnicola, 5; plants, 2.6; Arcellalike seeds, 1.4; algæ, 0.2; unknown, 2.

August 26.—Number examined, 1; length, 121. Food: Sialis nymphs, 85; sand, 5; unknown, 10.

August 28.—Number examined, 4; lengths, 118 to 132, average, 126. Food: Chironomid larvæ, 19.3; mayfly nymphs, 12.5; caddisfly larvæ, 2; chironomid pupæ, 2.5; Hyalella, 53.5; Physa, 6.2; plants, 1.2; sand, 0.5; bottom débris, 2; unknown, 0.3.

August 30.—Number examined, 8; lengths, 72 to 83, average, 77. Food: Chironomid larvæ, 9; mayfly nymphs, 14.3; chironomid pupæ, 4.4; Hyalella, 49.8; Chydorus, +; Eurycercus, 2.1; Ceriodaphnia, 18.1; plants, 0.6; Arcellalike seeds, 0.6; sand, 1.1.

September 1.—Spring Lake Creek; number examined, 7; lengths, 183 to 268, average, 216. Food: Fish, 2.9; chironomid larvæ, 0.1; caddisfly larvæ, 3.6; dragonfly nymphs, 85.5; Hyalella, 1; Physa, 3.3; Sphæriidæ, 1.4; Herbobdella, 1.1; plants, 2.

September 2.—Number examined, 1; length, 130. Food: Leptocerus larvæ, 5; plants, 95.

September 3.—Trot-line near bar; number examined, 6; lengths, 122 to 143, average, 134. Food: Sialis nymphs, 8; dragonfly nymphs, 10; chironomid pupæ, 4; crayfish, 10; Hyalella, 44; Ceriodaphnia, 4; oligochætes, 10; plants, 4; sand, 4; bottom débris, 2.

Summary.—Number examined, 43; lengths, 73 to 268, average, 112. Food: Fish, 0.5; insect larvæ, 34.1, insect pupæ, 8; mite, 0.5; crayfishes, 3.2; amphipods, 28.2; ostracods, +; cladocerans, 10.7; snails, 6.6; clams, 0.2; leeches, 0.2; oligochætes, 1.2; plants, 3.8; sand, 1; bottom débris, 0.4; unknown, 0.5.

The chief foods of the perch are insect larvæ, amphipods, and other crustaceans. It is worthy of note that the large perch caught on September 1 in Spring Lake Creek had eaten 85.5 per cent dragonfly nymphs. The perch's food in all habitats is largely from the bottom and from the aquatic vegetation.

Pimephales notatus (Rafinesque). Blunt-nosed minnow.

Three of these little minnows were examined, but only one contained food. This one was caught August 30, measured 52 mm. in length, and had eaten chironomid larvæ, 50, and chironomid pupæ, 50.

GENERAL REMARKS ON FOODS.

Arranged according to their use by all of the 15 species studied in Green Lake, the foods come in the following order: Insect larvæ (21.7), amphiphods (16.5), fish (9.6), crayfishes (7.8), cladocerans (7.6), insect pupæ (6.7), plants (4.5), snails (4.4), clams (4.1), insects (3.3), ostracods (3.3), sand (2.5), mud (2), oligochætes (0.6), leeches (0.5), unknown (0.4), mites (0.4), Mysis (0.3), algæ (0.2), copepods (0.1).

Sixty-seven and seven-tenths per cent of the food of the fishes of Green Lake is arthropods; 31.7 per cent, insects in all stages; and 35.6 per cent, crustaceans. About

85 per cent of the food comes from the bottom (65) and the water plants (30), leaving only one large item—the cladocerans—unassigned, and probably a portion of this item should be placed with the bottom and water plants. It is of course impossible to give exact figures in assigning animals used as food to particular habitats, but there is no doubt that the fishes get the greater part of their food from the bottom and from the shore vegetation. The open-water plankton (which to be sure is poor in this lake) is of little importance, except perhaps as food for the young of ciscoes and other fishes.

According to the ratios of particular foods consumed (during the period when observations were made), the fishes of Green Lake may be arranged as follows:

Fish.—Pickerel (97), yellow bullhead (32.5), smallmouth black bass (13.6), largemouth black bass (0.9), perch (0.5).

Insect larvæ.—Johnny darter (82.1), pumpkinseed (59.5), blunt-nosed minnow (50), perch (34), bluegill (33), smallmouth black bass (31.9), top-minnow (21.7), sucker (19), largemouth black bass (16.7), rock bass (11.8), yellow bullhead (10), speckled bullhead (3.8), carp (2), cisco (1.1).

Insect pupæ.—Blunt-nosed minnow (50), largemouth black bass (18.6), top-minnow (13.7), perch (8), smallmouth black bass (7.8), bluegill (1.7), rock bass (0.6).

Adult insects.—Yellow bullhead (24), bluegill (12.9), largemouth black bass (9.3), smallmouth black bass (5), sucker (0.3).

Mites.—Rock bass (4.2), speckled bullhead (0.5), blunt-nosed minnow (0.5), bluegill, +.

Crayfishes.—Rock bass (64), speckled bullhead (25.6), yellow bullhead (10), bluegill (9.2), largemouth black bass (4.1), perch (3.2).

Mysis.—Cisco (4.7).

Amphipods.—Cisco (61.2), sucker (40.7), top-minnow (35.2), perch (28.6), carp (25), largemouth black bass (18), bluegill (14.8), yellow bullhead (12.5), smallmouth black bass (4.1), rock bass (2.9), speckled bullhead (2.6), Johnny darter (2.5).

Cladocerans.—Smallmouth black bass (37.6), largemouth black bass (25.4), top-minnows (16.6), rock bass (12), carp (11), perch (10.7), yellow bullhead (1), speckled bullhead (0.1), bluegill (+).

Copepods.—Cisco (1.3).

Ostracods.—Carp (33), top-minnow (6.4), cisco (3), pickerel (1), sucker (0.7), rock bass (0.2), Johnny darter (0.1), largemouth black bass (0.1), perch (+).

Clams (all Sphæriidæ).—Sucker (29.9), carp (15), cisco (9.9), pumpkinseed (6.5), speckled bullhead (0.6), perch (0.2).

Snails.—Speckled bullhead (31.4), pumpkinseed (26.5), perch (6.6), cisco (0.8), bluegill (0.5), sucker (0.4).

Leeches.—Pumpkinseed (7.5), perch (0.2).

Oligochætes.—Speckled bullhead (7.2), perch (1.2).

Nematodes (*Gordiacean*).—Top-minnow (0.1).

Sponges.—Bluegill (0.5), sucker (0.3).

Plants.—Speckled bullhead (22), bluegill (21.3), yellow bullhead (10), largemouth black bass (5.2), perch (3.8), carp (3), pickerel (2), cisco (0.7), smallmouth black bass (0.2).

Algæ.—Bluegill (1.7), speckled bullhead (0.8).

Bottom ooze.—Carp (10), cisco (8.2), sucker (3), bluegill (2.2), perch (0.5).

Sand.—Johnny darter (15.3), top-minnow (5.9), sucker (5.7), rock bass (4.2), bluegill (2.2), carp (2), perch (1), smallmouth black bass (0.2), largemouth black bass (0.1).

Unknown.—Speckled bullhead (5.6), perch (0.4).

TABLE 8.—FOOD OF FISHES OF GREEN LAKE, AUG. 12 TO SEPT. 4, 1919.

Common and scientific name.	Number examined.	Average length in millimeters.	Fish.	Insect larvæ.	Insect pupæ.	Insects, adult.	Mites.	Crayfishes.	Mysis.	Amphipods.	Cladocerans.	Copepods.	Ostracods.
Bluegill, Lepomis incisor	18	165	......	33	1.7	12.9	+	9.2	......	14.8	+	......	......
Bullhead, speckled, Ameiurus nebulosus	9	302	......	3.8	......	......	0.5	25.6	......	2.6	0.1	......	......
Bullhead, yellow, Ameiurus natalis	2	280	32.5	10	......	24	......	10	......	12.5	1	......	......
Carp, Cyprinus carpio	1	133	......	2	......	......	......	......	......	25	11	......	33
Cisco, Leucichthys birgei	30	218	......	1.1	......	......	......	......	4.7	61.2	......	1.3	3
Johnny darter, Boleosoma nigrum	11	38	......	82.1	......	......	......	......	......	2.5	......	......	.1
Largemouth black bass, Micropterus salmoides	16	78	.9	16.7	18.6	9.3	......	4.1	......	18	25.4	......	.1
Minnow, blunt-nosed, Pimephalus notatus	1	52	......	50	50	......	......	......	......	......	......	......	......
Perch, Perca flavescens	43	112	.5	34.1	8	......	.5	3.2	......	28.6	10.7	......	+
Pickerel, Esox lucius	24	445	97	......	......	......	......	......	......	......	......	......	1
Pumpkinseed, Eupomotis gibbosus	5	146	......	59.5	......	......	......	......	......	......	......	......	......
Rock bass, Ambloplites rupestris	12	134	......	11.8	.6	......	4.2	64	......	2.9	12	......	.2
Smallmouth black bass, Micropterus dolomieu	11	114	13.6	31.9	7.8	5	......	......	......	4.1	37.6	......	......
Sucker, Catostomus commersonii	3	445	......	19	......	.3	......	......	......	40.7	......	......	.7
Top minnow, Fundulus diaphanus menona	12	44	......	21.7	13.7	......	......	......	......	35.2	16.6	......	6.4
Average	[1] 198	177	9.6	21.7	6.7	3.3	.4	7.8	.3	16.5	7.6	.1	3

Common and scientific name.	Clams.	Snails.	Leeches.	Oligochætes.	Nematodes.	Sponges.	Plants.	Algæ.	Bottom ooze.	Sand.	Unknown.
Bluegill, Lepomis incisor	......	0.5	......	......	......	0.5	21.3	1.7	2.2	2.2	......
Bullhead, speckled, Ameiurus nebulosus	0.6	31.4	......	7.2	......	......	22	.8	......	......	5.6
Bullhead, yellow, Ameiurus natalis	......	......	......	......	......	......	10	......	......	......	......
Carp, Cyprinus carpio	15	......	......	......	......	......	3	......	10	2	......
Cisco, Leucichthys birgei	9.9	.8	......	......	......	......	.7	......	8.2	......	.3
Johnny darter, Boleosoma nigrum	......	......	......	......	......	......	......	......	......	15.3	......
Largemouth black bass, Micropterus salmoides	......	......	......	......	......	......	5.2	......	......	.1	......
Minnow, blunt-nosed, Pimephalus notatus	......	......	......	......	......	......	......	......	......	......	......
Perch, Perca flavescens	.2	6.6	0.2	1.2	......	......	3.8	......	.5	1	.5
Pickerel, Esox lucius	......	......	......	......	......	......	2	......	......	......	......
Pumpkinseed, Eupomotis gibbosus	6.5	26.5	7.5	......	......	......	......	......	......	......	......
Rock bass, Ambloplites rupestris	......	......	......	......	......	......	......	......	......	4.2	......
Smallmouth black bass, Micropterus dolomieu	......	......	......	......	......	......	.2	......	......	.2	......
Sucker, Catostomus commersonii	29.9	.4	......	......	......	.3	......	......	3	5.7	......
Top minnow, Fundulus diaphanus menona	......	......	......	......	+	......	......	......	......	5.9	......
Average	4.1	4.4	.5	.6	+	+	4.5	.2	2	2.5	.4

[1] Total.

Table 9 gives the foods eaten by the fishes caught in Lake Mendota during the time covered by the observations in Green Lake. It will be noted that a greater variety of fishes was caught in Lake Mendota (22:15), and that foods differ somewhat in the two lakes. Fishes in Green Lake eat an excess of: Amphipods (13.6), larval insects (11.4), oligochætes (5.6), clams (4.1), insect pupæ (0.4), mites (0.4), and Mysis (0.3). Those in Lake Mendota excel in: Adult insects (13.8), fish (7.2), algæ (5), plants (3.7), copepods (1.5), cladocerans (1.4), ostracods (0.7), bottom ooze (0.7), sand (0.3).

TABLE 9.—FOOD OF FISHES OF LAKE MENDOTA, AUG. 10 TO SEPT. 15, 1919.

Common and scientific name.	Number examined.	Average length in millimeters.	Fish.	Insect larvæ.	Insect pupæ.	Insect, adults.	Mites.	Crayfishes.	Amphipods.	Cladocerans.	Copepods.	Ostracods.
Bluegill, Lepomis incisor	4	127		0.5		11.2						
Bream, Notemigonus crysoleucas	2	96				75						
Bullhead, speckled, Ameiurus nebulosus	5	131		41.8	1			3	12	3.4	+	2
Bullhead, yellow, Ameiurus natalis	3	221		1.3				75	10	3	0.3	
Carp, Cyprinus carpio	7	383	35									
Cisco, Leucichthys sp.?	5	366		47	10.8	7.2				35		
Crappie, Pomoxis sparoides	6	131	16.6	13.3	10.8	19.2				16	4.2	6.6
Gar, Lepisosteus osseus	2	278	100									
Johnny darter, Boleosoma nigrum	10	46		62.9								
Largemouth black bass, Micropterus salmoides	7	135	45			10.7		12.1	13.4	.8		
Minnow, Notropis heterodon	6	58			47.5	51.7						
Perch, Perca flavescens[1]	50	166		20.1	3.3	.8	+	8.3	1	42.2	.1	
Pickerel, Esox lucius	5	408	93									
Pike, wall-eyed, Stizostedion vitreum	2	410	100									
Pumpkinseed, Eupomotis gibbosus	9	118		29.3	.5	4.2			3			29.5
Rock bass, Ambloplites rupestris	10	128		2		5		50	5.8	14		
Shiner, Pimephalus notatus	7	46				25.6				31.4	14.1	
Silversides, Labidesthes sicculus	7	59			53.6	5.7				40.1		
Smallmouth black bass, Micropterus dolomieu	4	356		.5		82.5			2.5			
Sucker, Catostomus commersonii	5	304		4.7					4	+	1.7	
Top minnow, Fundulus diaphanus menona	5	61		3.2	7	1.4			11.4	15	15	40
White bass, Roccus chrysops	6	235	12.2		.2	75						
Average	[2] 166	194	16.8	10.3	6.1	17.1	+	6.8	2.9	9	1.6	3.7

Common and scientific name.	Clams.	Snails.	Leeches.	Oligochætes.	Protozoa.	Plants.	Algæ.	Bottom ooze.	Sand.	Unknown.
Bluegill, Lepomis incisor		0.8		0.8		75.6	10			
Bream, Notemigonus crysoleucas							25			
Bullhead, speckled, Ameiurus nebulosus		.6	7			10.6	17.1	1.4	0.6	
Bullhead, yellow, Ameiurus natalis		1.7					10.1			1.3
Carp, Cyprinus carpio		32.8				2.8		27.9		
Cisco, Leucichthys sp.?										
Crappie, Pomoxis sparoides						13.3				
Gar, Lepisosteus osseus										
Johnny darter, Boleosoma nigrum							13.6	2.9	20.7	
Largemouth black bass, Micropterus salmoides						3.6	14.2			
Minnow, Notropis heterodon						.8				
Perch, Perca flavescens[1]	0.7	6.2		7.6		6.5	.5	.9		
Pickerel, Esox lucius						7				
Pike, wall-eyed, Stizostedion vitreum										
Pumpkinseed, Eupomotis gibbosus		11	5.9			5.5			11.1	
Rock bass, Ambloplites rupestris						10	3		11.2	
Shiner, Pimephalus notatus						14.3	10	4.3		
Silversides, Labidesthes sicculus										
Smallmouth black bass, Micropterus dolomieu						5		9.5		
Sucker, Catostomus commersonii		57			0.1	10	10	11.7		
Top minnow, Fundulus diaphanus menona						4			9	
White bass, Roccus chrysops						12.2				
Average	+	5	.6	.4	+	8.2	5.2	2.7	2.8	.1

[1] No perch were examined in 1919. These are figures for 1915 during the same season of the year. [2] Total.

TABLE 10.—COMPARISON OF FOODS EATEN BY FISHES OF GREEN LAKE AND LAKE MENDOTA, 1919.

	Green Lake.	Lake Mendota.		Green Lake.	Lake Mendota.		Green Lake.	Lake Mendota.
Fish	9.6	16.8	Cladocerans	7.6	9	Sponges	+	−
Insect larvæ	21.7	10.3	Copepods	.1	1.6	Protozoa	−	+
Insect pupæ	6.7	6.1	Ostracods	3	3.7	Plants	4.5	8.2
Adult insects	3.3	17.1	Clams	4.1	+	Algæ	.2	5.2
Mites	.4	+	Snails	4.4	5	Bottom ooze	2	2.7
Crayfishes	7.8	6.8	Leeches	.5	.6	Sand	2.5	2.8
Mysis	.3	−	Oligochætes	6	.4	Unknown	.4	.1
Amphipods	16.5	2.9						

It will be noted (Tables 8, 9, and 10) that the foods eaten in excess in Green Lake are largely those associated with the bottom; those most eaten in Lake Mendota are found for the most part in shallow water with plants, or in the open water. These differences are in part accounted for by the stagnation of the deeper water and in part by the greater abundance of food resources in the latter lake. In Lake Mendota there is an abundance of food in the deeper parts, but such supplies are not easily accessible to fishes in summer because there is no oxygen below 8 to 12 m. Birge and Juday have recently made observations with mud dredges which, with the earlier work of Birge (1897) and Marsh (1903), indicate clearly that there is actually less food in Green Lake, as regards both bottom fauna and plankton, than in Lake Mendota. There are some common fishes in Lake Mendota (silversides, crappie, gar, white bass) which are rare or absent in Green Lake. These "extra" fishes feed to a considerable degree on plankton, insects (in or on the surface of the water), and fishes. There is apparently no chance for them to be abundant in Green Lake.

DISCUSSION AND CONCLUSIONS.

Green Lake is a fine clear body of water, with sandy and pebbly shores, and great depth. Seventeen species of fishes were caught in it during the summer. The lake stratifies in summer, but the lower water always contains oxygen, and of course remains cool (5° C.).

Lake Mendota has nearly twice the area of Green Lake but is only a third as deep. It stagnates during the summer in its depths and a large part of its water is without oxygen for about three months. Notwithstanding this handicap, Lake Mendota has more than twice as many fishes (as judged by the catch per hour in gill nets) in a unit area.

During the summer the distribution of the fishes in Green Lake shows definite stratification. From the surface down to a depth of 10 m. all species of fishes caught in the lake, except adult ciscoes, were found; from 10 to 20 m. only large pickerel, smallmouth black bass, and suckers occurred; from 20 to 40 m. no fishes were caught; from 40 to 70 m. ciscoes were the only fishes caught, and were abundant. Reighard's (1915, p. 246) idea that ciscoes inhabit the intermediate water and are not caught in gill nets set on the bottom is no longer tenable in the light of results presented in this paper. A. R. Cahn has also caught many ciscoes in gill nets set on the bottom in Oconomowoc Lake.

While gill nets were being set in Green Lake, 22 species of fishes were caught in Lake Mendota by the same methods. There are, then, not only more individuals, but a greater number of species in Lake Mendota. There were no fishes caught in gill nets in this lake in the lower, stagnant water, except an occasional perch. Most fishes stay above the thermocline, where oxygen is plentiful but the water warm. The perch apparently congregate just above the thermocline and make short excursions into the stagnated region to take advantage of the food offered by the rich bottom fauna.

The most abundant species in each lake is one which feeds very largely from the bottom in deep water. In Green Lake this species is the cisco; in Lake Mendota, it is the perch. Both species are present in both lakes, but a single and different species is dominant in each lake. The cool water in the depths of Green Lake abounds with ciscoes; the perch is not abundant and, in fact, was never caught in deep water. Although ciscoes are present in Lake Mendota they are few in number and the perch is the abundant fish in deep water, except when stagnation forces it out during the summer (Pearse and Achtenberg, 1920). The perch appears to be about equally abundant in both lakes in shallow water.

There are perhaps two reasons why ciscoes are not abundant in Lake Mendota and why perch are comparatively scarce in Green Lake. These are concerned with temperature and food. The perch may live in shallow water at rather high temperatures, but because the summer stagnation has made Mendota unsuitable for ciscoes, it has also been able to dominate the deep water. To flourish, the cisco appears to require cold water in summer and finds ideal conditions in the depths of Green Lake. There appears to be no good reason why the perch should not occur in the deeper parts of Green Lake. Perhaps it has never crossed the "barren zone" between the depths of 20 and 40 m. Perhaps the "attractive" food which takes it to the bottom of Lake Mendota is lacking. The characteristic animals in the bottom of Lake Mendota are enormous numbers of midge larvæ (Corethra, Chironomus, Protenthes, etc.). Little clams, oligochætes, crustaceans, and protozoans are also present. On the bottom of Green Lake the fauna is much the same, except that the crustaceans (particularly amphipods) are very abundant and midge larvæ are few.

The relatives of the cisco are usually found in the depths of lakes and in the cooler parts of the ocean. The relatives of the perch are mostly found in shallow regions of fresh water. The ciscoes apparently invaded fresh water from the ocean as the glaciers receded and have remained in the cooler parts. The perch has probably migrated into the depths of lakes from adjacent shallow waters to take advantage of the abundant stores of food there. Reighard (1915, p. 242) even classifies the perch in his "Vegetation Community," though he also found it in deeper water in Douglas Lake.

Not only are the fishes which feed on the bottom most abundant in both lakes, but the animals found in or on the bottom are most used for food by all the fishes in the lakes; that is by all species of fishes considered together. In Lake Mendota, however, more plankton is consumed by the fishes than in Green Lake, and this probably for two reasons: (1) There is actually more plankton in the lake, and (2) a large portion of the bottom is not readily accessible on account of stagnation.

The shallow waters in the two lakes under consideration are quite different. Green Lake has sandy and stony shores, with comparatively little vegetation; Lake Mendota has varied shores and large numbers of aquatic plants. These differences are reflected in the two basses, the smallmouth being the common one in Green Lake and the largemouth in Lake Mendota. The smallmouth in Green Lake feeds largely on shallow water cladocerans, insect larvæ, and fishes. The most important foods of the largemouth in Lake Mendota during the summer are fishes, adult insects, crayfishes, amphipods, and algæ. In this lake the smallmouth partakes largely of *adult* insects. The largemouth apparently becomes the dominant bass because it feeds more during the summer, which is its chief growing period, on food which is found in the shore vegetation rather than on the bottom.

Why is it that Lake Mendota has a greater number and variety of fishes than Green Lake in spite of the fact that (1) it has half the volume and (2) that a considerable portion of its bottom with much food is cut off by stagnation for three months during each year? The writer has thought over the whole question with care and can see no answer except—mud. The thick layer of soft mud on the bottom of Lake Mendota is rich in organic materials and contains a very abundant fauna of detritus feeders.[1] The mud and its animals form an enormous store of organic material. This makes aquatic plants and plankton abundant; this in turn gives opportunity for fishes (silversides, etc.) which feed on pelagic organisms to flourish and makes those which feed on plants and small fishes more abundant. Green Lake is a fine, healthful habitat for fishes in somewhat the same way that a desert on land is healthful. Its possibilities are limited because it lacks mud. Rich "soil" is just as important for raising animals from aquatic pastures as it is for those on land. Petersen (1918) has recently made a similar generalization in regard to the ocean.[2]

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[1] Birge and Juday have found as many as 30,000 Corethra larvæ per square meter in the mud on the bottom of Lake Mendota.

[2] Dr. R. E. Coker, after reading the manuscript for this paragraph, suggests that the richness of food stores in a lake may perhaps be connected with the fertility of the soil in the surrounding drainage area. Dr. R. H. Whitbeck, professor of geography in the University of Wisconsin, assures the writer that the drainage basin of Green Lake is less fertile than that of Lake Mendota.

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